PROC. BIOL. SOC. WASH.
100(1), 1987, pp. 44–74

THE SUBGENERA OF THE CRAWFISH GENUS *ORCONECTES* (DECAPODA: CAMBARIDAE)

J. F. Fitzpatrick, Jr.

Abstract. —The genus *Orconectes,* the last major cambarid genus to be reevaluated following the major increase in species recognized in recent years, is divided into 10 subgenera. Besides the nominate subgenus, *Faxonius* Ortmann, 1905, is resurrected and the new names *Billecambarus, Buannulifictus, Crockerinus, Gremicambarus, Hespericambarus, Procericambarus, Rhoadesius,* and *Tragulicambarus* proposed. Each is diagnosed and the type species illustrated; six species-groups are recognized in *Crockerinus,* four in *Procericambarus,* and two each in *Buannulifictus, Gremicambarus* and *Hespericambarus,* with *Billecambarus* and *Tragulicambarus* being monotypic. The divisions are justified with a phylogenetic discussion of morphological, geographical, and to a lesser extent, temporal considerations.

In recent years all of the major genera in the Cambaridae, except *Orconectes,* have been reevaluated. The tremendous increase in the number of recognized species has almost mandated that the members of the larger genera be grouped into natural associations at levels lower than genus, assemblages which have been formally recognized as subgenera and/or "Sections." Hobbs (1969) began the current reassessments with a study of *Cambarus* in which he recognized several subgenera, erected the genus *Fallicambarus* for one divergent group of species and recognized the validity of *Hobbseus,* proposed by Fitzpatrick and Payne (1968). Hobbs then turned his attention to *Procambarus* and identified a number of subgeneric groupings within it (1972). *Fallicambarus* likewise was discovered to consist of two subgeneric-level assemblages (Hobbs 1973). Recently, Fitzpatrick proposed subgenera for the monogeneric Cambarellinae (1983). Also recent is a series of events beginning with Hobbs' (1981) discovery of a new group, *Distocambarus,* which was first proposed as a subgenus of *Procambarus,* soon elevated to generic rank (Hobbs and Carlson 1983), and then divided into two subgenera (Hobbs 1983).

Associated with these major revisions, the past two decades have seen miscellaneous reassignments of species groups, principally by the elevation of subgenera to genera (Fitzpatrick 1963, Bouchard 1972). Also a new subgenus was proposed to receive a disjunct species, newly-discovered, and assignable to *Cambarus* (Bouchard and Hobbs 1976), and the similarly erected genus *Bouchardina* Hobbs, 1977, was offered.

For 25 years I have been studying the members of the genus *Orconectes,* second only to *Procambarus* in the number of described species assigned to it. The species have been assembled into "Groups" and the latter into "Sections," but they are essentially the same divisions proposed by Ortmann (1905) and modified by Creaser (1934). The number of species assigned to this genus has nearly doubled since then, but there has been no comprehensive review of the interspecific relationships or an attempt to reorganize the species into groupings which reflect this added knowledge. There are still several taxa which are known to exist but await formal description; likewise uncertain are the precise limits of variation in many species (most recently noted by Cooper and Hobbs 1980:1–2). Only two small groups of the genus have been studied in detail (Fitzpatrick 1967, Hobbs and Barr 1972). Nonetheless, certain clearly related groups seem obvious, and in comparing them some phylogenetic trends are suggested.

The nomenclatorial history of *Orconectes* is relatively straightforward. First proposed for troglobitic animals and established upon characteristics which are essentially adaptations to the spelean environment, the genus was inadequately defined (Cope 1872). Most of the early writers followed Faxon's (1885) lead in rejecting the genus. In 1905, Ortmann offered a scheme of classification for North American (=Cambaridae) crawfishes in which he proposed several subgenera, one of which was *Faxonius* with *Astacus limosus* Rafinesque, 1817, the second species known from North America, the type species. Faxon (1914) vigorously rejected this system, but in the interim Fowler (1912) accepted *Faxonius* as a subgeneric name and designated *Orconectes inermis* Cope, 1872, as the type species of *Orconectes* Cope, 1872. In 1933, Creaser accepted *Faxonius,* elevated it to generic level, and proposed a new subgenus, *Faxonella,* to receive the quite divergent *Cambarus clypeatus* Hay, 1899.

In a major reorganization, Hobbs (1942) argued cogently and persuasively for the recognition of Ortmann's (1905) subgenera, but as genera, with the exceptions that *Faxonius,* as a subjective junior synonym, be replaced by *Orconectes.* Since then *Orconectes* has been accepted according to his definition with one notable exception. Creaser (1962) rejected many of Hobbs' arguments and proposed different generic assignments. Of interest here is only that *Orconectes* (sensu Hobbs) was divided into three equivalent "generic patterns": *Faxonius, Faxonella,* and *Orconectes* (s. s.). To the latter he assigned *Cambarus lancifer* Hagen, 1870, *Orconectes inermis* Cope, 1872, and *Astacus pellucidus* Tellkampf, 1844 "(with subspecies—if they are subspecies)" (1962:3); *Faxonella* contained *Cambarus clypeatus* and, presumably, *Orconectes* (*Faxonella*) *beyeri* Penn, 1950. In general his system was rejected in favor of Hobbs' with the exception that Fitzpatrick's (1963) formal elevation of *Faxonella* to generic status is commonly accepted. No other major changes in nomenclature have been suggested.

The synonymies at most levels in the present paper have been kept to a minimum for brevity's sake. The reader is referred to Hobbs' extensive synonymies (1974b) if more detailed information is required.

Taxonomic Characters in *Orconectes*

As is the case with most crawfishes, certain of the obvious external morphological features, useful for the recognition of species, are readily modified to adapt to the environmental conditions in which the animal lives. Such features are difficult to use in establishing intergroup relationships except in the broadest sense. On the other hand, structures associated with amplexus are less susceptible to environmental modification. In *Orconectes,* however, even these cannot be easily analyzed. For example, in the Propinquus Group, studied in detail by Fitzpatrick (1967), a number of interspecific "hybrids" are reported in the literature (Crocker 1957, Crocker and Barr 1968). But Fitzpatrick (1967) strongly implied that natural hybridization was a rare occurrence. Recently, Capelli and Capelli (1980) and Smith (1981b) reported "hybrids" between species that I propose should be assigned to separate subgenera (!) below.

I have no reason to question the veracity of the reports of any of the workers mentioned above. Yet I remain firmly convinced that no extensive interspecific hybridization occurs in *Orconectes* or any other crawfish genus. It is very difficult to conceive of a species retaining its identity without reproductive isolation. Too many data exist not to believe that there are many, many species of crawfishes in North America. Smith himself (1981b), as he offers an explanation of events leading to the possible origins of his specimens, acknowledges that the occurrence of his apparent hybrids is probably a transient one and related to the quite artificial situation of an introduction of members of an alien population of a previously allopatric species. When such events occur, I would expect responses not unlike the well documented one in *Bufo* (e.g., Blair 1941, Cory and Manion 1955). Possibly the most revealing facts related to hybridization are in the experimental data gathered by Tierney and Dunham (1984) which seem to indicate that inability to recognize a conspecific mate exists principally in species which, because of allopatry, lack a stimulus to develop isolating chemical cues; *naturally* sympatric populations are probably more accurate in mate selection. Berrill (1985) assembled data from laboratory-induced interspecific matings between *O. propinquus* and *O. rusticus,* two species in competition as the latter is expanding its range, which demonstrated that such crossings reduced significantly the reproductive success in both species (or more specifically, from a natural standpoint, in individuals unable to identify their own species), similar indeed to the *Bufo* situation.

Equally, statistics fail to provide clear indication of relationships. Structures associated with amplexus in crawfishes are very variable and extensive overlaps occur in meristic and morphometric data (Fitzpatrick 1967; Chambers et al. 1979, 1980; Tierney 1982). Sometimes sophisticated statistical methodology is overtly misleading. For example, when a local population of *O. propinquus* (Girard) was subjected to discriminant analysis of morphology, it seemed to consist of two distinct morphological groups; pleopod morphology was among the highest discriminant functions (Fitzpatrick and Pickett 1980). Shortly thereafter, Smith (1981a) extended the examination to a larger—geographically and numerically—data base and determined that the proposed separation of forms was not justified.

Despite these difficulties, it is still possible to discern certain morphological associations which enable the recognition of species groups. In first form males, the first pleopods are straight or curved with respect to the long axis of the appendage. One may determine the proportions of the terminal elements with respect to each other and to the appendage as a whole; the elements can range from subsetiform to stout and bladelike. In females, the degree of sculpture of the annulus ventralis can be described in generalities that lead to groupings compatible with those based on pleopod morphology. Although no longer are groupings recognized that are based upon such characters as the areola, the spinose ornamentation of the cephalothorax and the structure of the cheliped, they, too, often exhibit a similarity compatible with groupings based on structures associated with amplexus. Using these, a natural system of classification can be established.

Notes on the *Orconectes* Annulus

The seminal receptacle of the Cambaridae is a potentially very useful tool for the taxonomist. Despite this, it has received little attention. Without the artistic skills of Hobbs, our knowledge would be little advanced beyond the level of the early part of the century (Andrews 1906a, b). Perhaps the most comprehensive collation of annulus morphology is in Hobbs' checklist (1974b), but all of his species descriptions and many of his reviews contain realistic, detailed representations of the structure. Only one study of variation in *any* species has been made: for *O. propinquus* (Tierney 1982); and very few descriptive terms have been established for features of the annulus. Hobbs (1981: 10, fig. 4b) provided a labelled figure and a brief verbal discourse on its anatomy. Fitzpatrick (1983) added some observations especially pertinent to the pendulent annulus as found in the Cambarellinae. To discuss *Orconectes,* however, requires the addition of some terminology.

Hobbs' figure (1981:fig. 4b) is essentially that of a procambarid, not undesirable as most consider that the family arose from a procambaridlike ancestor. But in most *Orconectes* there are prominent tubercular or lobular elevations associated with the cephalolateral surfaces (the *cephalolateral prominences*). These may be united–to varying degrees–along the cephalomedian margin, or they may be separated by a depression of varying development which I propose to call the *trough.* I interpret the *fossa,* as illustrated by Hobbs (1981), to be the fundus of a pit formed by a deep ingression of the *sinus.* In many *Orconectes* there is a conspicuous transverse subovate depression, located caudal to the cephalolateral prominences but cephalic to the higher caudal margins and not traversing the entire width of the annulus. I suggest that this depression be called the *sulcus.* The relationships of the sinus and fossa to this sulcus seem to be significant. One need only to refer to Tierney's (1982) difficulties in the application of the word "groove" to appreciate the need for the introduction of such terminology.

Generic and Subgeneric Diagnoses of *Orconectes*

Family Cambaridae Hobbs, 1942
Subfamily Cambaridae Hobbs, 1942
Genus *Orconectes* Cope, 1872

Diagnosis.—"Antenna never with conspicuous fringe on mesial border. Third maxilliped with teeth on mesial margin of ischium. Mesial margin of palm of chela usually with row of less than 12 tubercles; lateral margin of fixed finger never bearing row of spiniform tubercles; opposable margin of dactyl seldom with prominent excision. Areola broad to obliterated at midlength. Ischium of third, rarely third and fourth, pereiopod with hook. Coxa of fourth pereiopod of male lacking caudomesial boss except in troglobitic members. First pleopod of first form male almost always symmetrical, never deeply withdrawn between bases of pereiopods nor concealed by dense setal mat extending from ventrolateral margins of sternum, and contiguous basally; terminal elements (usually 2, occasionally 3 in troglobitic members) highly variable in length and disposition—divergent, straight, or curved caudodistically or caudally; central projection never abruptly curved caudally at base nor forming arc of more than 90 degrees. Female with annulus ventralis immovable or slightly movable in troglobitic species; first pleopod usually present. Branchial formula 17 + ep." (Hobbs 1974a: 14–15).

Billecambarus, new subgenus

Figs. 1, 14a

Diagnosis.—(Based on first form male and female.) Body and eyes pigmented, latter well developed. Rostrum with small marginal spines, median carina absent. Cervical spines much reduced or absent; areola about 9.5 times longer than wide with 1 or 2 punctations across narrowest part, and constituting about 34–35% of total length of carapace; cephaloventral surface of carapace with small squamous tubercles; devoid of spines or tubercles in hepatic region. First pleopod of male ending in 2 terminal elements, elements short (about 15% total length of pleopod), subparallel, both curved caudodistally from base so that apices directed at angle of nearly 90° to main axis of basal portion of pleopod; mesial process slender; distal fourth of pleopod inclined caudodistally at angle of about 30°; shoulder on cephalic surface of pleopod just proximal to aforementioned inclination not strongly developed or sharply angular. Inner margin of palm of chela about 28.5% of length of outer margin; opposable margins of immovable finger and dactyl with prominent

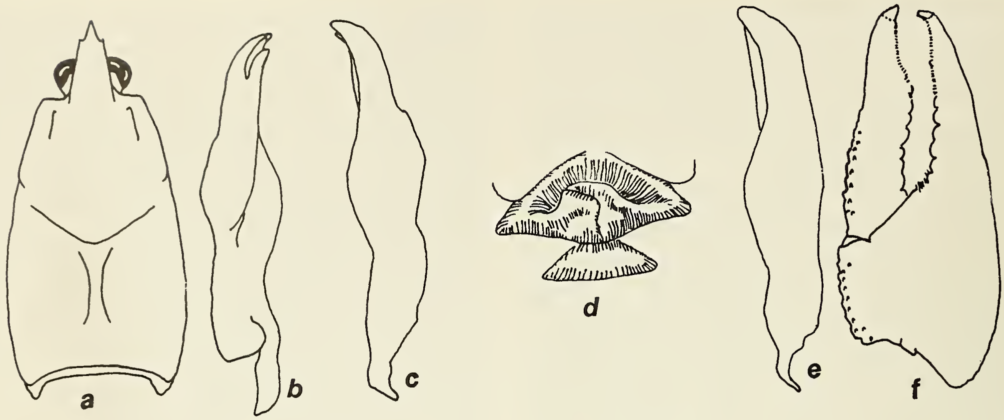


Figure 1

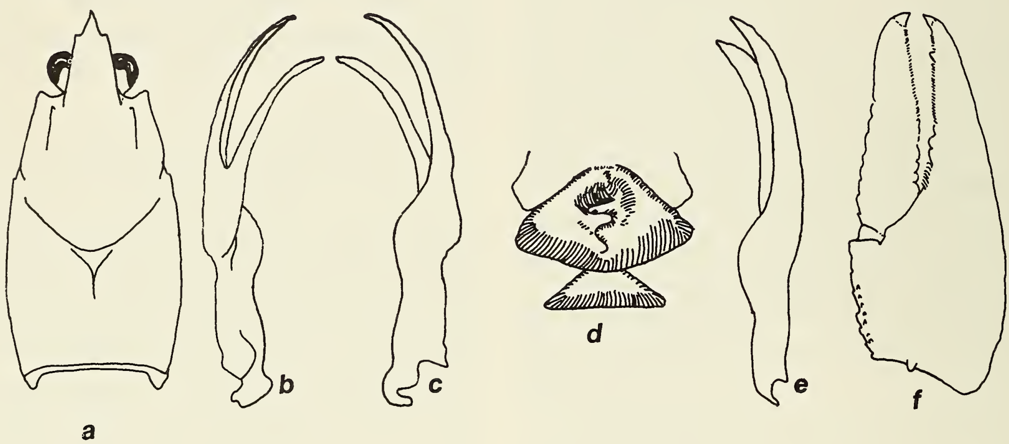


Figure 2

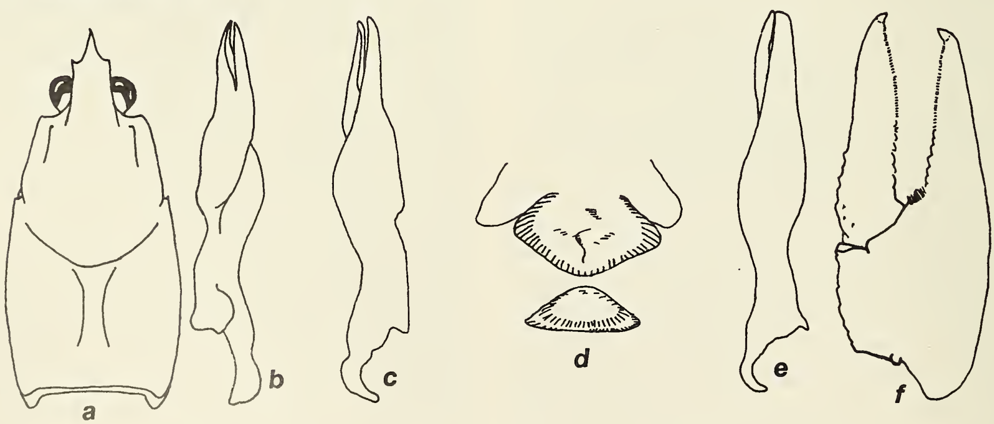


Figure 3

subequal tubercles in basal half; tuft of setae at base of immovable finger, if present, quite weakly developed. Annulus ventralis of female immovable, firmly attached to preceding sclerite, widest near midlength and only slightly more than twice as wide as long; cephalolateral prominences tuberculiform and narrow; sulcus deep and arching through 80% of cephalic half of annulus; fossa not conspicuous with sinus traversing deep depression inclined at angle of about 20° to transverse axis about midpoint of annulus, then turning sharply caudally following shallower depression to caudal margin.

Type species.—*Cambarus Harrisonii* Faxon, 1884:130.

List of species.—Monotypic, *Orconectes* (*Billecambarus*) *harrisonii* (Faxon, 1884: 130).

Gender.—Masculine.

Etymology.—*Bille* (German = axe) plus the generic name, *Cambarus,* because the first pleopod of the male reminds me of a bill-hook used in pruning plants.

Buannulifictus, new subgenus
Figs. 2, 13b

Diagnosis.—(Based on first form male and female.) Body and eyes pigmented, latter well developed. Rostrum with marginal spines, lacking median carina. Cervical spines if present reduced; areola obliterated, linear, or with room for no more than 2 punctations in narrowest part, constituting 31–36% total length of carapace; cephaloventral surface of carapace with small squamous tubercles; devoid of spines or tubercles in hepatic region. First pleopod of male ending in 2 terminal elements of subequal length (except in *O. m. meeki*), moderately long (36–45% total length of pleopod), and both curved caudodistally throughout length (except in *O. m. meeki*), mesial process subsetiform; cephalic margin of pleopod lacking shoulder. Inner margin of hand 28–31% of length of outer margin; opposable margin of immovable finger with prominent (except in *O. palmeri creolanus*), subequal tubercles in basal half; opposable margin of dactyl with prominent (except in *O. p. palmeri, O. p. creolanus,* and *O. hobbsi*), subequal tubercles; tuft of setae at base of immovable finger not well developed but present in most specimens of *O. palmeri* subspp. Annulus ventralis of female immovable, firmly attached to preceding sclerite, widest caudal to midlength and about as wide as long; cephalolateral prominences lobiform and weakly developed in most specimens; sulcus when obvious sharply constricted laterally but obvious central depression always present; trough usually present but not deep or conspicuous; sinus originating in fossa set at acute angle to longitudinal axis of annulus and winding sinuously caudad but lost before reaching caudal margin.

Type species.—*Cambarus Palmeri* Faxon, 1884:124.

List of species.—Palmeri Group (areola linear or obliterated; central projection more than 40% of total length of pleopod):

Orconectes (*Buannulifictus*) *denae* Reimer and Jester, 1975:124.
O. (*B.*) *hobbsi* Penn, 1950:381.
O. (*B.*) *palmeri palmeri* (Faxon, 1884:124).
O. (*B.*) *palmeri creolanus* (Creaser, 1933: 16).

←

Figs. 1–3. Type species of *Orconectes* subgenera (all not to same scale): 1, *Orconectes* (*Billecambarus*) *harrisoni*; 2, *O.* (*Buannulifictus*) *palmeri palmeri*; 3, *O.* (*Crockerinus*) *sanbornii sanbornii*. a, Dorsal view of carapace; b, Mesial view of first pleopod of first form male; c, Lateral view of first pleopod of first form male; d, Annulus ventralis of female; e, Lateral view of first pleopod of second form male; f, Dorsal view of chela of first form male.

O. (*B.*) *palmeri longimanus* (Faxon, 1898: 655).

Meeki Group (areola with room for at least one punctation across narrowest part; central projection less than 40% of total length of pleopod):

Orconectes (*Buannulifictus*) *meeki meeki* (Faxon, 1898:657).
O. (*B.*) *meeki brevis* Williams, 1952:348.

Gender.—Masculine.

Etymology.—*Bu*- (L., =large, prefix) + *annulus* (L., =ring) + *fictus* (L., =form), an allusion to the large annulus ventralis characteristic of members of this subgenus.

Crockerinus, new subgenus
Figs. 3, 13a

Description.—(Based on first form male and female.) Body and eyes pigmented, latter well developed. Rostrum with marginal spines, median carina present or absent. Cervical spines usually present and moderately well developed; areola 4–10 times longer than wide with room for more than 2 punctations in narrowest part, constituting 29–36% total length of carapace; cephaloventral surface of carapace with small squamous tubercles, devoid of spines or tubercles in hepatic region. First pleopod of male ending in 2 terminal elements of subequal length or with mesial process slightly shorter, moderately long (29–36% of total length of pleopod), subparallel (except in *O. shoupi*); basal half of both elements subparallel to main axis of pleopod, distal half continuing subparallel to axis or curved caudodistally about 45°; mesial process subsetiform; cephalic margin of pleopod with or without shoulder. Inner margin of hand 29–36% length of outer margin; opposable margins of both fingers with or without prominent tubercles in basal half, tubercles always subequal in size; small tuft of setae at base of immovable finger present or absent. Annulus ventralis of female immovable, firmly attached to preceding sclerite, widest at or slightly cephalic to midlength and 1.6–2.1 times wider than long; cephalolateral prominences lobiform or tuberculiform, moderately or well developed; sulcus varying from shallow and obscure to well developed (not developed in *O. bisectus, O. shoupi,* and *O. tricuspis*); trough present and well developed to absent; fossa when present small but deep (linear in *O. illinoiensis*), located near midpoint of annulus, sinus usually moving sharply laterally and then recurving to near midline before progressing sinuously caudad but lost before reaching caudal margin (except in *O. erichsonianus*).

Type species.—*Cambarus Sanbornii* Faxon, 1884:128.

List of species.—Sanbornii Group (central projection 24–29% total length of pleopod, distal half straight—except extreme tip often arced caudally—and subparallel to mesial process; lacking distinct gap between bases of fingers; opposable margin of fixed finger usually with one tubercle larger than rest; annulus 1.4–1.7 times wider than long, moderately developed cephalolateral prominences oriented at distinct angle to transverse axis, trough obscure, and sinus originating near midpoint of annulus and with distinctly laterally oriented section in anterior half):

Orconectes (*Crockerinus*) *obscurus* (Hagen, 1870:69).
O. (*C.*) *sanbornii sanbornii* (Faxon, 1884: 128).
O. (*C.*) *sanbornii erismophorus* Hobbs and Fitzpatrick, 1962:208.
O. (*C.*) *stannardi* Page, 1985:564.
O. (*C.*) *virginiensis* Hobbs, 1951:122.

Marchandi Group (central projection 28–29% total length of pleopod, distal half straight or curved caudodistally—*marchandi*—and subparallel to mesial process; lacking distinct gap between bases of fingers; opposable margin of fixed finger usually with one tubercle larger than rest; annulus 1.5–1.6 times wider than long, well developed cephalolateral prominences oriented at distinct angle to transverse axis, trough well developed, and sinus originating near midpoint of annulus and lacking distinctly laterally oriented section in anterior half):

Orconectes (*Crockerinus*) *eupunctus* Williams, 1952:330.
O. (*C.*) *marchandi* Hobbs, 1948b:140.

Propinquus Group (central projection 30–35% total length of pleopod, distal half straight—except extreme tip sometimes arced caudally—and subparallel to mesial process; lacking—except in *jeffersoni*—distinct gap between bases of fingers; opposable margin of fixed finger without one tubercle larger than rest; annulus 1.7–1.9 times wider than long, weakly to moderately developed cephalolateral prominences oriented at distinct angle to transverse axis, trough weakly or only moderately developed, and sinus originating near to or just lateral to midpoint of annulus and distinctly laterally oriented section in anterior half):

Orconectes (*Crockerinus*) *erichsonianus* (Faxon, 1898:659).
O. (*C.*) *jeffersoni* Rhoades, 1944:123.
O. (*C.*) *propinquus* (Girard, 1852:88).

Rafinesquei Group (central projection 21–29% total length of pleopod, distal half straight—except extreme tip often arced caudally—and subparallel to mesial process; lacking distinct gap between bases of fingers; opposable margin of fixed finger with or without one tubercle larger than rest; annulus 1.6–1.8 times wider than long, cephalolateral prominences lobiform or broadly tuberculiform and always well developed, oriented—often as much as 90°—at distinct angle to transverse axis, trough distinct and usually moderately deep, and sinus may or may not originate in deep fossa near or slightly lateral to midpoint of annulus before following undulant longitudinal route not quite to caudal margin, sinus with—except in *bisectus*—distinctly laterally oriented section in anterior half):

Orconectes (*Crockerinus*) *bisectus* Rhoades, 1944:129.
O. (*C.*) *illinoiensis* Brown, 1956:163.
O. (*C.*) *rafinesquei* Rhoades, 1944:116.
O. (*C.*) *tricuspis* Rhoades, 1944:117.

Shoupi Group (central projection about 21% total length of pleopod, straight, subparallel to mesial process in basal half but distal half of latter curved caudodistally at angle of about 45° and not subsetiform; distinct gap between bases of finger about as wide as width of base of dactyl; opposable margin of fixed finger without one tubercle larger than rest; annulus about 2.4 times wider than long, well developed tuberculiform cephalolateral prominences oriented subparallel to transverse axis and occupying much of cephalic half of annulus, trough narrow but distinct, sinus originating on midline in cephalic third of annulus, arcing caudolaterally to point caudolateral to middle of annulus, recurving to midpoint before turning sharply caudadally to proceed in substraight line almost to caudal margin):

Orconectes (*Crockerinus*) *shoupi* Hobbs, 1948a:14.

Gender.—Masculine.

Etymology.—Named in honor of Denton W. Crocker in recognition of his lifelong study of many of the species assigned to this subgenus.

Subgenus *Faxonius* Ortmann, 1905:97
Figs. 4, 15a

Faxonius (subgeneric name): Ortmann, 1905 (part).—Fowler, 1912 (part).
Faxonius (generic name): Creaser, 1933 (part); 1962 (part).
[For a fuller synonymy and explanation see Hobbs 1942:339, 350–352; 1974a:14; 1974b:26.]

Diagnosis.—(Based on first form male and female.) Body and eyes pigmented, latter well developed. Rostrum with marginal spines, median carina absent. Cervical spines well developed (except in *O. indi-*

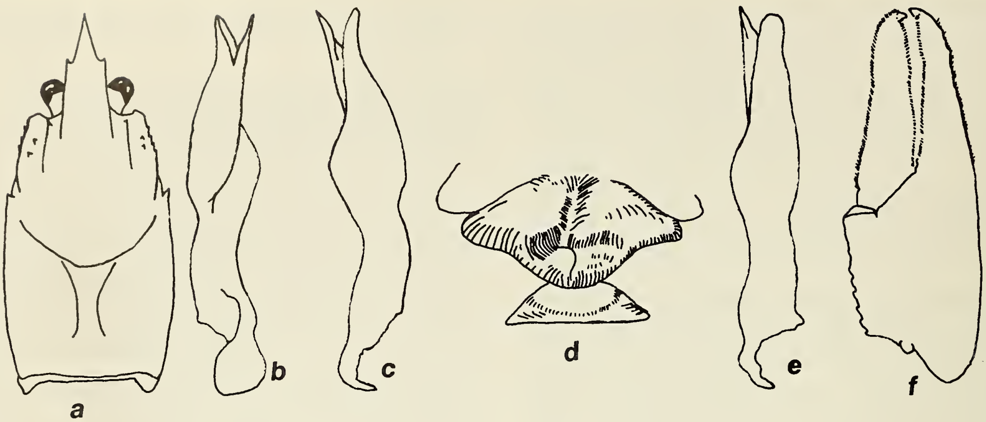


Figure 4

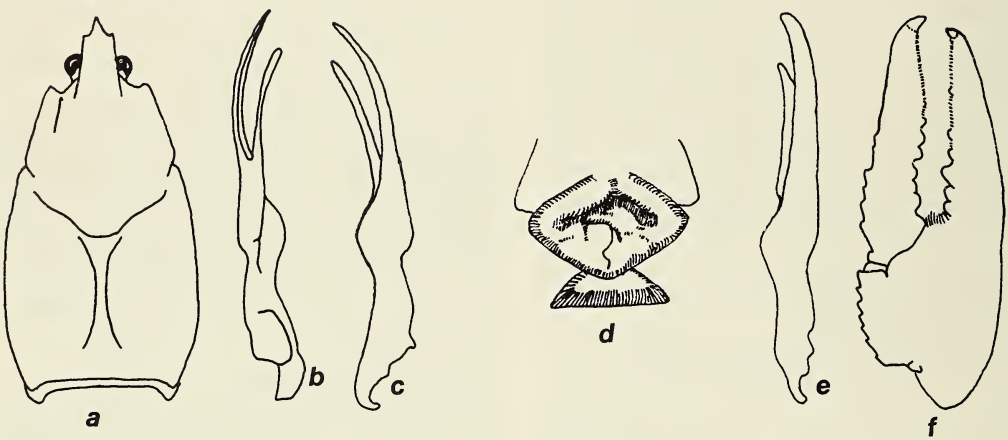


Figure 5

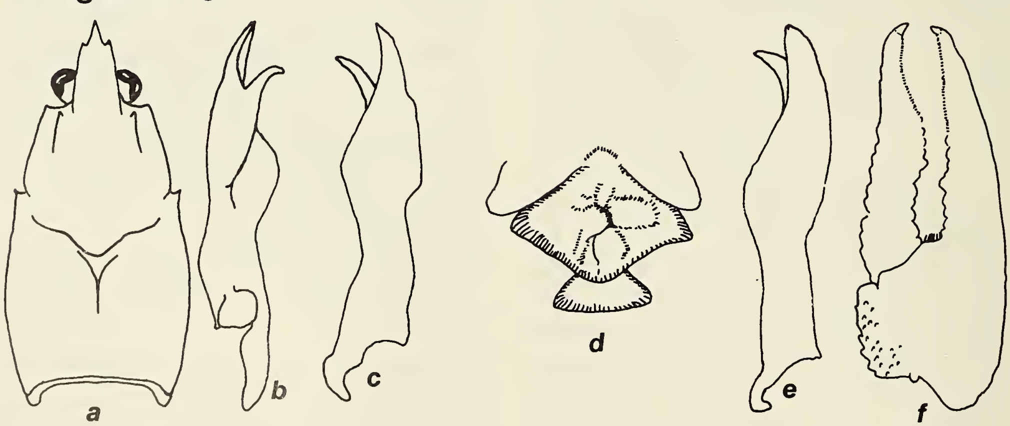


Figure 6

anensis); areola 6.0–8.0 times longer than wide with room for more than 2 punctations in narrowest part, and constituting 31–33% total length of carapace; cephaloventral surface of carapace with small squamous or spinose tubercles, hepatic region with (in *O. limosus*) or without spines. First pleopod of male ending in 2 terminal elements of subequal length, short (less than 20% total length of pleopod), straight but divergent at angle of about 20°, neither (except central projection in *O. wrighti*) subparallel to main axis of pleopod; mesial process slender and tapering apically but not subsetiform; distal half of pleopod (except in *O. wrighti*) slightly inclined caudodistally; cephalic margin of pleopod lacking shoulder. Inner margin of hand 33–40% length of outer margin; opposable margins of fingers lacking prominent tubercles in basal half, setose margins obscuring small tubercles; tuft of setae at base of immovable finger lacking. Annulus ventralis of female immovable, firmly attached to preceding sclerite, widest near midlength and 1.9–2.1 times wider than long; cephalolateral prominences tuberculiform and well developed, occupying much of cephalolateral half of annulus; sulcus arising lateral to midline of annulus then moving to it before turning sharply caudally forming only very slightly undulant line disappearing before reaching caudal margin.

Type species.—*Astacus limosus* Rafinesque, 1817:42. Designated by Ortmann 1905: 97.

List of species.—

Orconectes (*Faxonius*) *indianensis* (Hay, 1896:494).

O. (*F.*) *limosus* (Rafinesque, 1817:42).

O. (*F.*) *wrighti* Hobbs, 1948c:85.

Gremicambarus, new subgenus
Figs. 5, 12

Diagnosis.—(Based on first form male and female.) Body and eyes pigmented, latter well developed. Rostrum with or without marginal spines, median carina absent (except in *O. alabamensis*). Cervical spines much reduced, absent, or only moderately well developed; areola obliterated, linear or to 3.5 times longer than wide with room for more than 2 punctations in narrowest part of wider areolae, constituting 25–40% total length of carapace; cephaloventral surface of carapace with small squamous tubercles; devoid of spines and tubercles in hepatic region. First pleopod of male ending in 2 terminal elements, elements moderately long to long (20–40% total length of pleopod), subparallel or divergent with central projection subparallel to main axis of pleopod through at least 90% length or curved caudodistally or inclined caudodistally; elements subequal in length with mesial process tapering evenly from base to tip or deflected sharply caudodistally (to 90°) in apical 15% with distal part subspatulate and cephalically excavated; cephalic surface of pleopod lacking shoulder. Inner margin of hand 25–43% length of outer margin; opposable margin of immovable finger with or without (*O. alabamensis, O. compressus, O. rhoadesi*) row of prominent tubercles in basal half and if present one markedly larger than rest; opposable margin of dactyl also with tubercles likewise disposed except one never markedly larger than rest; tuft of setae of varying degree of development present at base of immovable finger (except in *O. compressus* and *O. mississippiensis*). Annulus ventralis of female immovable, firmly attached to preceding sclerite, widest near

←

Figs. 4–6. Type species of *Orconectes* subgenera (all not to same scale): 4, *Orconectes* (*Faxonius*) *limosus*; 5, *O.* (*Gremicambarus*) *virilis*; 6, *O.* (*Hespericambarus*) *difficilis*. a, Dorsal view of carapace; b, Mesial view of first pleopod of first form male; c, Lateral view of first pleopod of first form male; d, Annulus ventralis of female; e, Lateral view of first pleopod of second form male; f, Dorsal view of chela of first form male.

midlength (except caudal to midlength in *O. alabamensis*) and (except in *O. alabamensis* and *O. immunis*) length and width subequal; cephalolateral prominences well developed and occupying most of width of annulus; trough of varying width and depth but always clearly evident; sulcus deep, usually partially overhung along some of its width by caudal parts of cephalolateral prominences; fossa deep although sometimes obscured by overhang of cephalolateral prominences with sinus originating lateral to midline in cephalic half of annulus and moving transversely across midline where making U-shaped turn to midline and thence caudad for varying distance but never so far as caudal margin of annulus.

Type species.—*Cambarus virilis* Hagen, 1870:63.

List of species.—Virilis Group (central projection greater than 35% total length of pleopod and reaching coxa of first pleopod; mesial process subsetiform or tapering base to tip; caudal margin of annulus somewhat angular):

Orconectes (*Gremicambarus*) *causeyi* Jester, 1967:518.
O. (*G.*) *nais* (Faxon, 1885:140).
O. (*G.*) *virilis* (Hagen, 1870:63).

Alabamensis Group (central projection less than 35% total length of pleopod and reaching no farther anteriorly than coxa of second pleopod; mesial process apically subspatulate; caudal margin of annulus generally rounded):

Orconectes (*Gremicambarus*) *alabamensis* (Faxon, 1884:125).
O. (*G.*) *chickasawae* Cooper and Hobbs, 1980:29.
O. (*G.*) *compressus* (Faxon, 1884:127).
O. (*G.*) *cooperi* Cooper and Hobbs, 1980:17.
O. (*G.*) *etnieri* Bouchard and Bouchard, 1976b:459.
O. (*G.*) *holti* Cooper and Hobbs, 1980:23.
O. (*G.*) *immunis* (Hagen, 1970:71).
O. (*G.*) *mississippiensis* (Faxon, 1884:123).
O. (*G.*) *rhoadesi* Hobbs, 1949:19.
O. (*G.*) *validus* (Faxon, 1914:382).

Gender.—Masculine.

Etymology.—*Gremius* (Latin = middle, center) in combination with the generic name, *Cambarus,* an allusion to the dominance of this subgenus in the central part of North America.

Hespericambarus, new subgenus
Figs. 6, 16a

Diagnosis.—(Based on first form male and female.) Body and eyes pigmented, latter well developed. Rostrum with marginal spines, median carina absent. Cervical spines well developed; areola obliterated and constituting 31–33% total length of carapace; cephaloventral surface of carapace with small squamous tubercles; devoid of spines or tubercles in hepatic region (except small spines in *O. blacki*). First pleopod of male terminating in 2 elements, elements short (less than 20% total length of pleopod) and unequal in length (except in *O. blacki* and *O. maletae*), apices divergent with longer central projection subparallel to main axis of pleopod or deflected caudodistally to angle of 45°, mesial process deflected 30–90°; shoulder present on cephalic surface of pleopod only in *O. difficilis.* Inner margin of hand 24–31% length of outer margin; opposable margins of immovable finger and dactyl with prominent subequal tubercles in basal half (*O. difficilis* with one, centrally located, larger than rest on both fingers); tuft of setae small but obvious at base of immovable finger. Annulus ventralis of female immovable, firmly attached to preceding sclerite, widest at midlength or nearly so, about as wide as long; cephalolateral prominences lobiform or obscure with poorly defined trough visible only in *O. difficilis* and *O. hathawayi*; sulcus-like structure evident only in *O. maletae* and there caused by single cephalomedian prominence; fossa if present poorly defined and sinus describing simple undulant line in caudal half of annulus but not reaching caudal margin.

Type species.—*Cambarus difficilis* Faxon, 1898:656.

List of species.—Difficilis Group (mesial process sharply recurved and approaching subsetiform; central projection slender; anterior portion of sinus of annulus deeply incised):

Orconectes (*Hespericambarus*) *difficilis* (Faxon, 1898:656).
O. (*H.*) *maletae* Walls, 1972:456.

Hathawayi Group (mesial process broad and tapering from base to tip, not recurved more than 45°; central projection laterally compressed; sinus of annulus shallowly incised):

Orconectes (*Hespericambarus*) *blacki* Walls, 1972:454.
O. (*H.*) *hathawayi* Penn, 1952:1.
O. (*H.*) *perfectus* Walls, 1972:451.

Gender.—Masculine.

Etymology.—*Hesperius* (Latin = western) in combination with the generic name, *Cambarus,* referring to the generally western distribution of the members of this subgenus.

Subgenus *Orconectes* Cope, 1872:419
Figs. 7, 8, 16b

Orconectes: Cope, 1872.—Fowler, 1912.—Hobbs, 1942.—Creaser, 1962 (part).
Faxonius: Ortmann, 1905 (part) (subgeneric name).—Creaser, 1933 (part) (subgeneric name).
[For a fuller synonymy and explanation see Hobbs 1942:339, 350–352; 1974a:14; 1974b:26.]

Diagnosis.—(Based on first form male and female.) Albinistic; eyes reduced and without pigment. Rostrum with or without marginal spines; median carina absent. Cervical spines well developed to scarcely observable; areola 3.5–6.5 times longer than wide with room for more than 2 punctations across narrowest part, constituting 34–46% total length of carapace; cephaloventral surface of carapace usually with small spinose or squamous tubercles; hepatic region usually (except in *O. inermis testii*) with one to many spines of varying degrees of development. First pleopod of male ending in 2 or 3 very short (less than 10% total length of pleopod) terminal elements, caudal process if present always small and often vestigal; mesial process tapering from base to tip, divergent distally and usually subequal in length to central projection (but in *O. pellucidus* mesial process at least twice as long as central projection); central projection more or less subparallel to main axis of pleopod; rounded shoulder (often angular but always small in *O. australis packardi*) present in *O. australis* subspp. and *O. incomptus* but absent in *O. inermis* subspp. and *O. pellucidus.* Inner margin of hand 37–39% length of outer margin; opposable margin of immovable finger with at least one small tubercle in basal half, usually more and (except in some specimens of *O. pellucidus*) with one larger than rest; opposable margin of dactyl with 3–5 small tubercles in basal half but only *O. australis* subspp. with one larger than rest. Annulus ventralis of female slightly movable, always separated from preceding sclerite by nonsclerotized cuticle, widest at or slightly cephalic to midlength or with measurements subequal; cephalolateral prominences in strict sense absent but prominent longitudinal ridges along midline occupying cephalic two-thirds or more of annulus; ridges usually separated by narrow shallow median groove probably representing trough; sometimes shallow transverse depression associated with caudal margins of aforementioned ridges perhaps representing rudimentary sinus; fossa if present poorly developed and sinus usually arising anterior to it in caudal fourth of

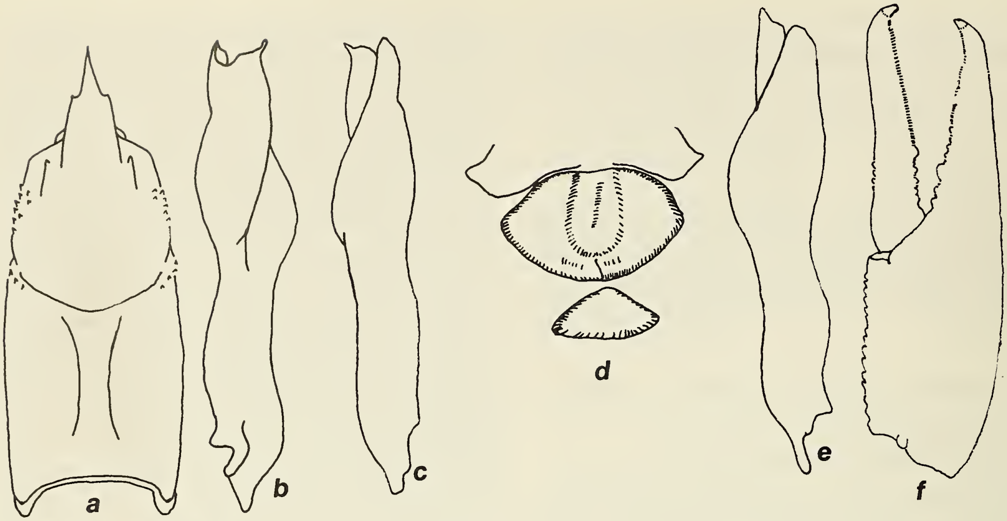


Figure 7

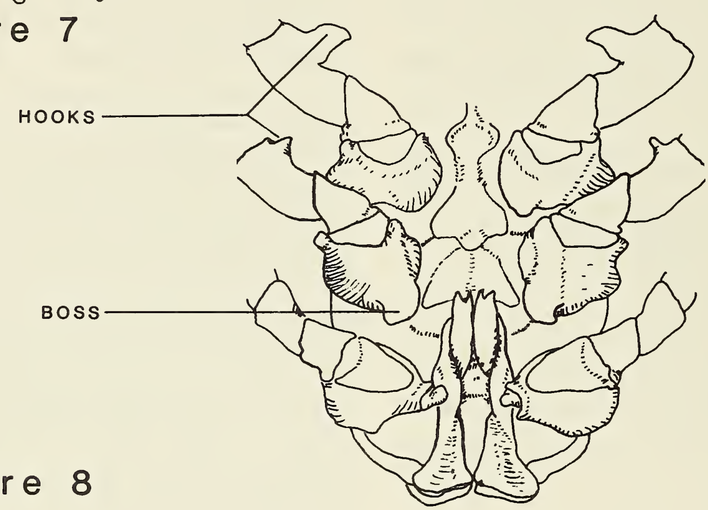


Figure 8

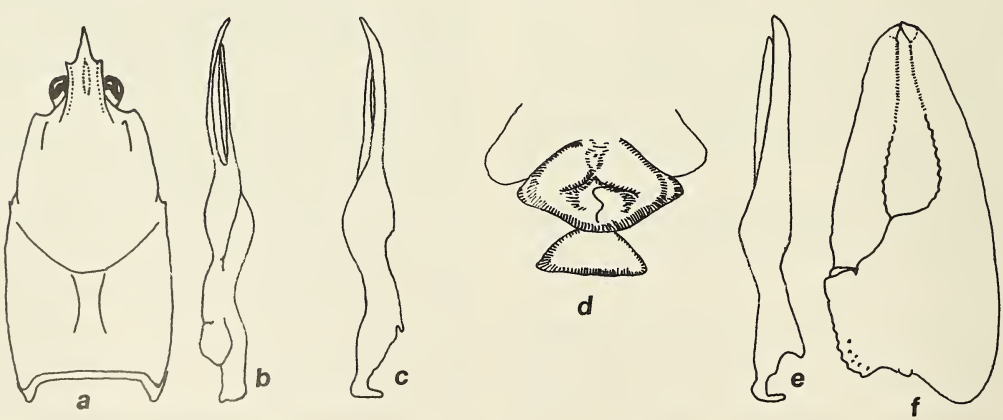


Figure 9

annulus near midline and arcing gently to or nearly to caudal margin.

Type species.—*Orconectes inermis* Cope, 1872:449; designated by Fowler 1912:339 as type-species of the genus *Orconectes*.

List of species.—

Orconectes (*Orconectes*) *australis australis* (Rhodes, 1941:142).
O. (*O.*) *australis packardi* Rhoades, 1944: 121.
O. (*O.*) *incomptus* Hobbs and Barr, 1972: 32.
O. (*O.*) *inermis inermis* Cope, 1872:449.
O. (*O.*) *inermis testii* (Hay, 1891:148).
O. (*O.*) *pellucidus* (Tellkampf, 1844:684).

Procericambarus, new subgenus
Figs. 9, 17

Diagnosis.—(Based on first form male and female.) Body and eyes pigmented, latter well developed. Rostrum with marginal spines or distinctly angular cephalic termini of margins so that bases of acumen clearly delimited; median carina present or absent. Cervical spines present and well developed to scarcely observable; areola 4.5–17.5 times longer than wide with room for at least 2 and usually more punctations across narrowest part, and constituting 29–37% total length of carapace; cephaloventral surface of carapace with small squamous tubercles; devoid of spines or tubercles in hepatic region. First pleopod of male ending in 2 terminal elements, elements long (34–55% total length of pleopod) and of subequal length or with central projection 10–20% longer than mesial process, subparallel or very slightly divergent (artifactual divergence in preserved specimens not uncommon); central projection subsetiform, straight and subparallel to main axis of pleopod or gently arced, apical 5–10% curved sharply caudodistally or distally so that apex directed nearly 90° to main axis of basal part of pleopod; mesial process subsetiform and apex rounded distally (except subspatulate and cephalically excavated in *O. nana* and *O. macrus*), usually subparallel to main axis of pleopod for most of length but distal 10–20% often arced cephalodistally; cephalic surface of pleopod with or without prominent sharply angled shoulder just proximal to base of central projection. Inner margin of hand 24–38% length of outer margin; opposable margin of immovable finger with prominent tubercles in basal half (except in *O. forceps* and *O. mirus*), only rarely (in *O. longidigitus* and *O. williamsi*) with one larger than remainder; opposable margin of dactyl with small or low scale-like tubercles (except prominent in *O. longidigitus, O. ozarkae,* and *O. williamsi,* and unequal in size), all subequal in size; tuft of setae if present at base of immovable finger poorly developed, prominent only in *O. ozarkae.* Annulus ventralis of female immovable, firmly attached to preceding sclerite, widest near midlength and distinctly wider than long if caudal overhang present in some species not considered; cephalolateral prominences large and lobiform (except reduced to low ridges in *O. quadruncus*); trough distinct and usually deep (except in *O. ozarkae, O. quadruncus* and some specimens of *O. longidigitus*); sulcus deep and obvious (shallow but usually distinct in *O. quadruncus*), cephalic parts often obscured by overhang of cephalolateral prominences; sinus arising in distinct deep fossa (fossa sometimes obscured by overhanging ceph-

←

Figs. 7–9. Type species of *Orconectes* subgenera (all not to same scale): 7 and 8, *Orconectes* (*Orconectes*) *inermis inermis*; 8, ventral view of posterior thorax of first form male (redrawn from Hobbs and Barr 1972); 9, *O.* (*Procericambarus*) *forceps*. a, Dorsal view of carapace; b, Mesial view of first pleopod of first form male; c, Lateral view of first pleopod of first form male; d, Annulus ventralis of female; e, Lateral view of first pleopod of second form male; f, Dorsal view of chela of first form male.

alolateral prominences) in cephalic part of sulcus, curving sharply laterad, executing U-turn at midline, then extending sinuously caudad to disappear before reaching caudal margin.

Type species.—*Cambarus forceps* Faxon, 1884:133.

List of species.—Forceps Group (terminal elements of pleopod of unequal length, central projection 34–40% total length of pleopod, both elements subsetiform; cephalic shoulder present or absent; annulus about twice as wide as long, caudal margin rounded—except in *O. neglectus chaenodactylus*—and with overhanging cephalolateral prominences creating large sulcal cavity):

Orconectes (*Procericambarus*) *barrenensis* Rhoades, 1944:125.
O. (*P.*) *forceps* (Faxon, 1884:133).
O. (*P.*) *longidigitus* (Faxon, 1898:653).
O. (*P.*) *mirus* (Ortmann, 1931:81).
O. (*P.*) *neglectus neglectus* (Faxon, 1885: 142).
O. (*P.*) *neglectus chaenodactylus* Williams, 1952:344.
O. (*P.*) *placidus* (Hagen, 1870:65).
O. (*P.*) *rusticus* (Girard, 1852:88).

Hylas Group (terminal elements of pleopod of markedly unequal length, central projection 48–52% total length of pleopod and subsetiform, mesial process subsetiform or apex bluntly rounded or apex expanded and cephalically excavate; cephalic shoulder present; annulus about as long as wide or slightly longer than wide and with caudal margin produced into tongue-like projection which overhangs following sclerite);

Orconectes (*Procericambarus*) *acares* Fitzpatrick, 1965:87.
O. (*P.*) *hylas* (Faxon, 1890:632).
O. (*P.*) *leptogonopodus* Hobbs, 1948b:146.
O. (*P.*) *peruncus* (Creaser, 1931:7).
O. (*P.*) *punctimanus* (Creaser, 1933:1).

Quadruncus Group (terminal elements of pleopod subequal in length, central projection about 33% total length of pleopod and tapering from base to tip, mesial process spatulate and excavated cephalically in distal third with small spinose projection in distal fourth of caudal margin, both elements inclined caudally in distal half; cephalic shoulder absent; annulus about as wide as long with caudal margin projected into tongue-like protrusion which overhangs following sclerite, cephalolateral prominences and sulcus weakly developed):

Orconectes (*Procericambarus*) *quadruncus* (Creaser, 1933:10).

Spinosus Group (terminal elements of pleopod of unequal length, central projection 40–48% total length of pleopod, both elements subsetiform; cephalic shoulder present—absent only in *O. williamsi*; annulus at least as long as wide, caudal margin rounded and if projected only slightly overhanging following sclerite):

Orconectes (*Procericambarus*) *luteus* (Creaser, 1933:7).
O. (*P.*) *macrus* Williams, 1952:337.
O. (*P.*) *medius* (Faxon, 1884:121).
O. (*P.*) *menae* (Creaser, 1933:5).
O. (*P.*) *nana* Williams, 1952:333.
O. (*P.*) *ozarkae* Williams, 1952:339.
O. (*P.*) *putnami* (Faxon, 1884:131).
O. (*P.*) *saxatilis* Bouchard and Bouchard, 1976a:439.
O. (*P.*) *spinosus* (Bundy, 1877:175).
O. (*P.*) *transfuga* Fitzpatrick, 1966a.
O. (*P.*) *williamsi* Fitzpatrick, 1966b.

Gender.—Masculine.

Etymology.—*Procerus* (Latin = tall, thin) combined with the generic name, *Cambarus,* an allusion to the long, thin terminal elements characteristic of most members of this subgenus.

Rhoadesius, new subgenus
Figs. 10, 14b

Diagnosis.—(Based on first form male and female.) Body and eyes pigmented, latter well developed. Rostrum with marginal

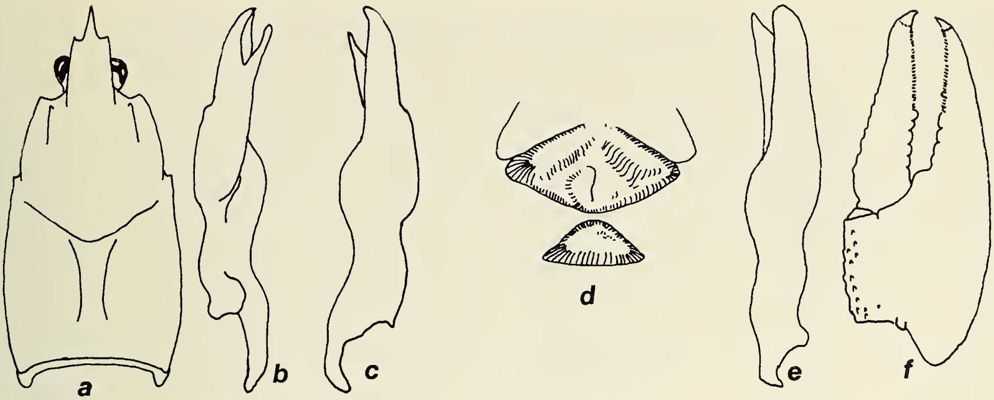


Figure 10

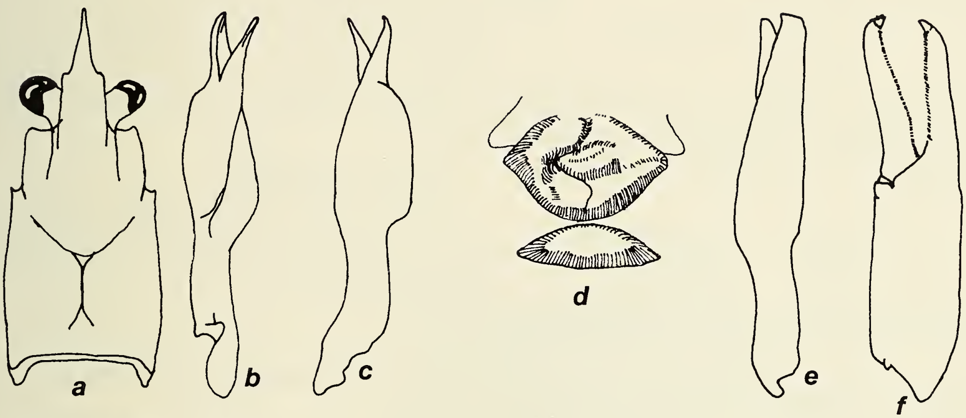


Figure 11

Figs. 10, 11. Type species of *Orconectes* subgenera (all not to same scale): 10, *Orconectes* (*Rhoadesius*) *sloanii*; 11, *O.* (*Tragulicambarus*) *lancifer.* a, Dorsal view of carapace; b, Mesial view of first pleopod of first form male; c, Lateral view of first pleopod of first form male; d, Annulus ventralis of female; e, Lateral view of first pleopod of second form male; f, Dorsal view of chela of first form male.

spines, median carina absent. Cervical spines well developed; areola 5.5–6.5 times longer than wide with 3–4 punctations across narrowest part, and constituting 32–34% total length of carapace; cephaloventral surface of carapace with small squamous tubercles; devoid of spines or tubercles in hepatic region. First pleopod of male ending in 2 short (less than 18% total length of pleopod) terminal elements of unequal length, elements subparallel (*O. sloanii*) or divergent (*O. kentuckiensis*), mesial process stout and tapering from base to tip; distal half of pleopod inclined caudodistally at angle of about 30° to main axis of basal portion; cephalic surface of pleopod with (*O. sloanii*) or without (*O. kentuckiensis*) shoulder. Inner margin of hand about 29% length of outer margin; opposable margin of immovable finger and dactyl with (*O. sloanii*) or without (*O. kentuckiensis*) prominent tubercles, never with one more strongly developed than others; tuft of setae at base of immovable finger, if present, never well developed. Annulus ventralis of female immovable, firmly attached to preceding sclerite; widest near midlength; cephalolateral prominences developed only in *O. sloanii* and trough not always clearly demonstrated; sulcus usually present but often not well defined; sinus arising near midpoint of annulus, in well defined fossa only in *O. kentuckiensis,* and following simple undulating path to be lost before reaching caudal margin.

Type species.—*Cambarus sloanii* Bundy, 1876:24.

List of species.—

Orconectes (*Rhoadesius*) *kentuckiensis* Rhoades, 1944:122.
O. (*R.*) *sloanii* (Bundy, 1876:24).

Gender.—Masculine.

Etymology.—Named in honor of the late Rendell Rhoades in recognition of his contributions to our knowledge of crawfishes.

Tragulicambarus, new subgenus
Figs. 11, 15b

Orconectes: Creaser, 1962:3 (part), 6 (Fig. 15), 7 (part).

Diagnosis.—Based on first form male and female.) Body and eyes pigmented, latter well developed. Rostrum lacking marginal spines but with sharply angular shoulders delimiting base of very long (about 50% of total length of rostrum) acumen, median carina absent. Cervical spines well developed; areola obliterated and constituting about 31% total length of carapace; cephalolateral surface of carapace with small squamous tubercles; devoid of spines or tubercles in hepatic region. First pleopod of male ending in 2 short (about 18% of total length of pleopod) terminal elements of subequal length; central projection subparallel to main axis of pleopod and laterally compressed into blade-like structure; mesial process stout, tapering from base to tip and divergent from central projection throughout length; cephalic surface of pleopod with well defined shoulder near base of central projection. Inner margin of hand about 45% length of outer margin; opposable margin of immovable finger and of dactyl without prominent tubercles; margins of fingers setose but tuft of setae at base of immovable finger lacking. Annulus ventralis of female immovable, firmly attached to preceding sclerite; widest near midlength and about as long as wide; cephalolateral prominences well developed and separated by well defined trough; sulcus deep but only unilaterally developed; sinus arising in distinct fossa in sulcus and lateral to midline of annulus, moving caudomesially in gentle arc to midline, there turning caudally to traverse slightly undulant path to intersect caudal margin.

Type species.—*Cambarus lancifer* Hagen, 1870:59.

List of species.—Monotypic, *Orconectes* (*Tragulicambarus*) *lancifer* (Hagen, 1870: 59).

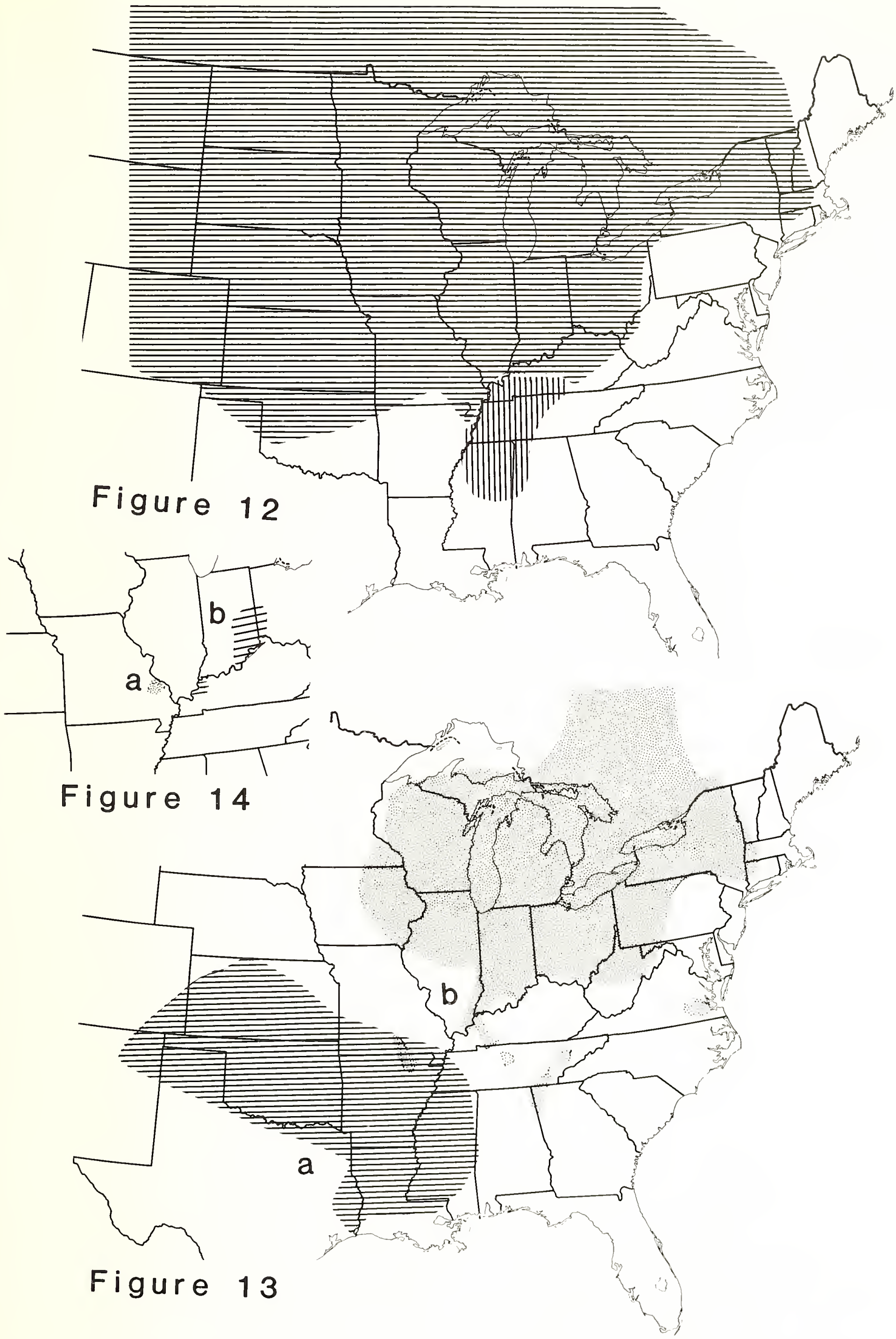
Gender.—Masculine.

Etymology.—*Tragula* (Latin = a javelin) combined with the generic name, *Cambarus,* a reference to the trivial name of the only species.

Phylogenetic Considerations
Fig. 18

As outlined above, the similarities of taxonomic characters in *Orconectes* make it difficult to apply cladistic techniques rigidly when considering phylogeny. Nevertheless, one can make some outgroup and ingroup comparisons to identify probable apomorphies and plesiomorphies. The latter comparisons are sometimes confusing, because ecological channelization has led to convergent emergences of certain characteristics.

Perhaps the clearest plesiomorphy is multiple terminal elements. Hobbs has convincingly argued for a procambarid-like ancestor for the family Cambaridae (1958, 1967, 1969, 1976, 1981; Hobbs and Barr 1960, 1972). Implicit in these discussions is an ancestral pleopod of four elements, from which certain lineages can be shown



Figs. 12–14. Distribution of *Orconectes* subgenera: 12, Subgenus *Gremicambarus* (horizontal rulings = contribution of *virilis-nais* complex; vertical rulings = other species of the subgenus); 13, Subgenera *Buannulifictus* and *Crockerinus* (a, horizontal rulings = *Buannulifictus*; b, stippling = *Crockerinus*); 14, Subgenera *Billecambarus* and *Rhoadesius* (a, stippling = *Billecambarus*; b, horizontal rulings = *Rhoadesius*).

Figure 15

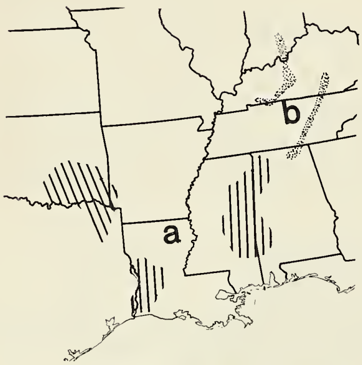


Figure 16

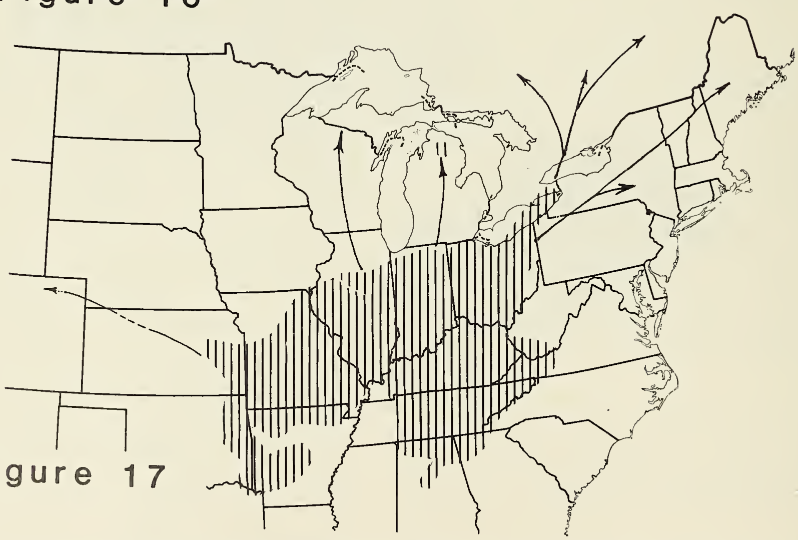


Figure 17

Figs. 15–17. Distribution of *Orconectes* subgenera: 15, Subgenera *Faxonius* and *Tragulicambarus* (a, vertical rulings = *Tragulicambarus*; b, stippling = *Faxonius*); 16, Subgenera *Hespericambarus* and *Orconectes* (a, vertical rulings = *Hespericambarus*; b, stippling = *Orconectes*); 17, Subgenus *Procericambarus* (arrows represent probable or actual introductions where large populations have been established, probably at the expense of native species).

to lose specific elements. Also, in general, these elements are fundamentally short in the plesiomorphic state.

Identification of the first clade.—The retention of short (comparatively) terminal elements by members of the subgenus *Orconectes* is the more primitive form. This conclusion is reinforced by the presence of a third element (the caudal process) in *O.* (*O.*) *australis australis* and in *O.* (*O.*) *incomptus* and the occasional presence of a vestigial caudal process in *O.* (*O.*) *australis packardi* (in some specimens even a vestigial cephalic process can be recognized: Hobbs and Barr 1972:31, fig. 8c, d). Hooks (sometimes rudimentary) on the fourth pereiopods of specimens of *O.* (*O.*) *australis* subspp., *O.* (*O.*) *inermis* subspp., and *O.* (*O.*) *pellucidus* further serve to place the subgenus close to the stem population from which the genus descended. (Only in rare specimens of other subgenera of *Orconectes* are hooks found on pereiopods other than the third.)

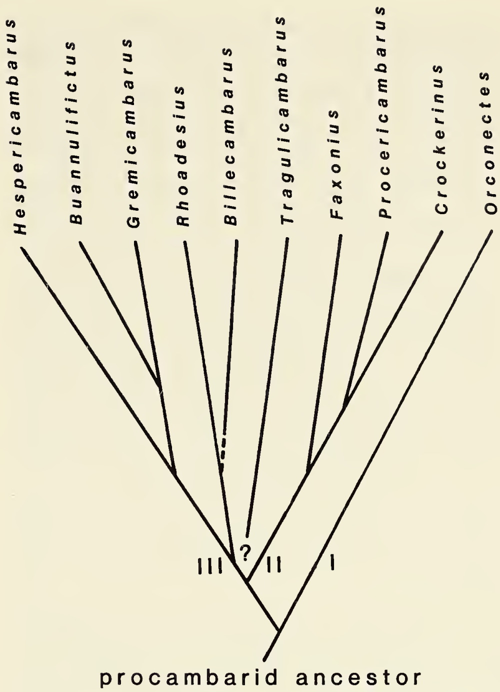


Fig. 18. Cladogram expressing proposed relationships of subgenera of *Orconectes.*

Other features attributed to the procambarid ancestor also present in the nominate subgenus include spinose ornamentation of the hepatic region of the carapace and along the cephalic part of the cervical groove, a short broad areola, and a movable (albeit slightly) annulus ventralis in the females. Equally significant is the presence of these apparently most primitive members of the genus in a geographical area which Hobbs (most recently, 1984) considers the center of diversity for the Cambaridae; members of the subgenus are troglobites in the karst along the southeastern edge of the Cumberland Plateau. Thus, by outgroup comparisons one is able to establish reasonably reliable plesiomorphic character states for the genus, identify the group retaining the greatest number of plesiomorphic states, and postulate probable lineages through which the several subgenera were established. Unfortunately, of these, only the terminal elements of the male pleopod and the annulus ventralis of the female are not subject to influence by the habitat. And the most striking feature of the annulus in the subgenus *Orconectes,* its motility, is lost in all other subgenera.

Enough plesiomorphies do exist, however, to permit evaluations of other character states in the members of the nominate subgenus and to compare them with members of *Procambarus* which Hobbs (1984) has indicated contain many familial plesiomorphies: the subgenera *Pennides* and *Ortmannicus* (particularly the Pictus Group). From these comparisons, one can project additional probable synapomorphies for the genus.

In those species with the greatest number of plesiomorphies (*O. australis* subspp. and *O. incomptus*) a shoulder is present at the cephalic base of the central projection. A similarly situated or somewhat proximally displaced irregularity (in varying degrees of development) can be found in some members of *Pennides* (*P. ablusus, P. lylei, P. natchitochae, P. versutus*) and some members of the Pictus Group (*P. enoplosternum,* *P. hirsutus, P. pictus*). Fitzpatrick (1967) postulated that the shoulder was plesiomorphic for members now assigned to the subgenus *Crockerinus,* which members likewise exhibit few character states which I consider apomorphic. Thus, a cephalic shoulder would seem to be plesiomorphic, but not its degree of development.

The annuli ventrales of members of *Pennides* and the Pictus Group of *Ortmannicus,* although not as simply constructed as the *Orconectes* in question, are nevertheless comparatively weakly sculptured as a group. Further, females of the genus *Cambaroides* (subfamily Cambaroidinae) have only a simple, unsculptured annular plate. It is not, therefore, excessive to consider more elaborate sculpturing of this structure to be apomorphic.

In *Orconectes* one can find no consistent pattern of cheliped development which can be used to establish lineages. This feature was extremely useful to Hobbs (1969) when he examined *Cambarus.* Equally, the carapaces of *Orconectes* species do not afford a means to evaluate apomorphic trends. In most carapace characteristics, the members of the genus are remarkably similar.

If one accepts the postulates I have offered, then some decisions about lineages can be made. In members of the subgenus *Orconectes* the annulus ventralis is movable, nearly planar and, significantly, lacking any structures which can be identified unequivocally as vestiges or precursors of a trough or sulcus. The central projection and mesial process are both short; the former is often flattened in the cephalocaudal plane and the mesial process is usually robust although tapering from base to tip. When compared with these character states and with members of other genera of the Cambaridae, long subsetiform elements, bladelike central projections, and spatulate, cephalically excavated mesial processes become the apomorphic condition.

The first recognizable apomorphies seem to be a firm commitment in the gonopod to only two terminal elements (the central projection and the mesial process), their elongation, and the introduction of orconectid (for lack of a better term) sculpturing to the annulus ventralis. Shortly after these specializations become established, in group II of my cladogram (that leading to *Crockerinus, Faxonius,* and *Procericambarus*), the main shaft of the pleopod became more cylindrical, principally through the reduction of the caudal expansion of that area situated caudolateral to the proximal opening of the sperm groove. At about the same time, development of both a trough and sulcus occurred on the annulus, and the mesial process of the male gonopod became subsetiform.

In group III there was no appreciable reduction of the caudal expansion of the gonopod, it remained rather prominent; the mesial process tended toward attenuation but was not subsetiform. In females, the trough and sulcus were probably very weakly developed and variable.

Trends leading to Faxonius.—Returning to group II, further developments can be recognized. The divergent apices of the terminal elements of the gonopod were retained by some, as were the plesiomorphic carapace spines (evidenced by their retention in *O. limosus*), and a clearly recognizable trough can be seen; only in *O. wrighti* is the sulcus obscure, but in all of them the cephalolateral prominences are easily identifiable, and the sinus arises in a barely recognizable fossa near the midwidth of the sulcus. The populations diversified into the members of the subgenus *Faxonius.*

Other populations of group II took another tack (leading to *Crockerinus* and *Procericambarus*). The central projection also approached a subsetiform state, and the straight elements moved into a subparallel relationship. A shoulder was probably present on the pleopod (Fitzpatrick 1967:167), and both trough and sulcus were clearly evident on the annulus.

Trends leading to Crockerinus.—Of these, those that developed into members of the subgenus *Crockerinus* retained a relatively low degree of relief on the surface of the annulus; the sinus arose from a moderately developed fossa which was located near the midline of the annulus in the cephalic portion of the sulcus. From there, the sinus usually extended laterad or caudolaterad before recurving sharply to the midline (the unique annulus of *O. bisectus* is an exception); and from there it followed a gently sinuous path nearly to the caudal margin, only rarely (in *O. erichsonianus* and *O. shoupi*) intersecting it. A fundamentally broadly spindled shape was retained throughout.

The male gonopods remained in a more conservative state. They were longer than the plesiomorphic condition found in members of the subgenus *Orconectes* and longer than in members of the subgenus *Faxonius* but somewhat shorter than the conditions found in members of the subgenus *Procericambarus.* Both the mesial process and central projection became less stout, but they remained subequal in length or nearly so. The central projection never reached a state of being subsetiform. The cephalic shoulder was lost in most populations, but individuals in many retained it, albeit usually in a reduced form.

Trends leading to Procericambarus.—In members of *Procericambarus* the annulus developed large, conspicuous cephalolateral prominences and a deep, distinct trough, often overhung in its cephalic parts by the cephalolateral prominences; in general, the annuli of members of *Procericambarus* are the most prominently sculptured in the genus. The strong tongue-like projection of the caudal margin of the annulus in members of the Hylas Group also represents an extreme for the genus. The terminal elements of the male gonopod became much elongated, especially the central projection. The tip of the elements reach the coxae of the second pereiopod when the abdomen is flexed, and in some species they reach as far as the mouthparts. Undoubtedly, in pleopods one can say that the most divergent state of the genus is reached. The subgenus seems to represent the most modified, with respect to structures used in amplexus, situation in the genus, and indeed its members may well be the most specialized members of the family in this respect.

Trends leading to Tragulicambarus.—Returning to the initial dichotomy of the two major groups, an enigma, *O. lancifer,* is encountered. In many ways it is unlike any other *Orconectes.* The acumen usually accounts for at least half of the total length of the rostrum, although I have seen many specimens in which the acumen approached more typical proportions. The hand is long and narrow, the inner margin of the palm being clearly longer than the dactyl. The central projection is laterally compressed and blade-like, a characteristic shared only with *O. bisectus.* But all of these, except the pleopod, probably represent specializations rather than significant apomorphies. The hand is very reminiscent of *Procambarus* (*Capillicambarus*) spp. and less so of *Faxonella* spp. All of these species inhabit roadside ditches or other such semipermanent standing waters. The hand would seem to be more indicative of habitat than ancestry. Never reaching the extreme of *lancifer,* the acumena of several apparently distantly related species of *Orconectes* can be quite long: *O.* (*O.*) *inermis, O.* (*C.*) *virginiensis, O.* (*P.*) *longidigitus.* Likewise, outgroup representatives sometimes have very long acumena: *Cambarellus* (*Cs.*) *prolixus, Procambarus* (*Ortmannicus*) *youngi, P.* (*Pennides*) *ablusus, P.* (*Pe.*) *lylei, P.* (*Pe.*) *lagniappe.* Such distribution discourages the use of the acumen to determine relationships.

If the general morphology of the pleopod of *lancifer* is compared with what I have taken to be the plesiomorphic condition, one notices that the reduction of the area caudolateral to the proximal opening of the sperm groove is not reduced to the degree found in members of *Crockerinus, Faxo-*

nius, and *Procericambarus.* In this respect, the pleopod is more like that of the lineage of group III of the major dichotomy than of group II. Similarly, the length of the cephalocaudal axis of the annulus is nearly equal to that of the transverse axis, again more like the condition obtaining in the group III stem. Discounting the apparently environmentally influenced features, *Tragulicambarus* seems to have arisen as a unique divergence from the group III stock, but its precise relationship remains unclear.

Less tenuous are the lineages of what I perceive to be the principal line of descent in the group III arm of the dichotomy. The greatest diameter of the gonopod remained located just distal to the proximal opening of the sperm groove, and there it retained close to twice the diameter at the base of the terminal elements. In the terminal elements, especially the mesial process, a marked tendency to have their apices oriented caudodistad or caudad developed. The length of the cephalocaudal axis of the annulus approached or slightly exceeded that of the transverse axis. The development of cephalolateral prominences encouraged the appearance of distinct troughs and sulci.

Trends leading to Hespericambarus.—The species which digressed least from the postulated ancestral type of group III are assigned to the subgenus *Hespericambarus.* In these animals, the terminal elements retained a relatively stout condition, were still relatively short and had minimal modification of their basic shape. The annuli were simple, and in none was the combination of a clearly defined trough and sulcus present. Only in *O. difficilis* (and possibly *O. maletae*) is a fossa present, and the sinus, although more conspicuous than that in the subgenus *Orconectes,* is not elaborate. Moreover, only in *O. difficilis* does the cephalocaudal elongation of the annulus become such that the structure can be described as subrhomboid. *Orconectes hathawayi* seems to be the extant species which can be described as "closer to the ancestral type." It has the straightest and shortest terminal elements in the subgenus; but also pertinent is the fact that many individuals bear spines (although most rather small) in the hepatic region of the carapace, their presence earlier herein considered a plesiomorphic character state.

As a final observation, I should comment on the nomenclature employed for members of this subgenus. Lacking contrary evidence, I would retain the nomenclatorial combinations proposed by Walls (1972), despite that fact that I cannot comprehend the intergradations of populations visualized by him. But for reasons implicit in my recognizing two "Groups" within the subgenus, I am listing each taxon as a distinct species and deferring determination of the precise limits of variations for the several populations until a later time.

Trends leading to Rhoadesius.—Probably closely related to but nonetheless distinct from *Hespericambarus* is the small group of crawfishes assigned to the subgenus *Rhoadesius.* These differ from members of the former principally in that the distal half of the pleopod is inclined caudally to the main axis of the appendage (as established by the basal part). The annuli are relatively simple, but in *O. kentuckiensis* a fossa is present, and in *O. sloanii* ridge-like cephalolateral prominences suggest a tendency to sulcus formation. Both species have a moderately broad areola in contrast to the obliterated one in members of *Hespericambarus,* yet this character is unreliable for determining relationships. Species, in any genus, which inhabit cool, tumbling waters tend to have a short, broad areola; in contrast, species living in sluggish, warm, standing waters and burrowers most likely will have a long and obliterated areola; species living in intermediate type habitats usually exhibit intermediate characteristics of this structure.

Trends leading to Billecambarus.—Perhaps the most confusing of the members of the genus is *O.* (*Billecambarus*) *harrisoni.*

In some respects the pleopod resembles that of members of *Rhoadesius,* but the short terminal elements are curved throughout their length to a degree that, coupled with caudal inclination of the distal half of the pleopod, the apices of both are directed due caudad. The annulus is unique in the genus. Only in *O.* (*R.*) *kentuckiensis* are the cephalolateral regions so undeveloped that the anterior half of the annulus is essentially a deep transverse excavation similar to the condition in *O.* (*Bi.*) *harrisoni.* In the latter, this transverse sulcus (?) is overhung caudally by a median projection of the more elevated caudal half; the sinus originates nearly on the cephalolateral margin and runs obliquely in a deep groove to the midline before turning caudally to move in a scarcely arched path to the caudal margin. The species seems to be a digressive, trans-Mississippi offshoot of *Rhoadesius.*

Trends leading to Gremicambarus.—In members of the subgenus *Gremicambarus* the central projection is straight in its basal part, although the distal parts of the pleopods are frequently inclined caudally with respect to the main axis of the basal half of the appendage. The mesial process is likewise usually straight basally. The proportions of the annulus approach those of *Crockerinus,* but the structures differ conspicuously from those of the latter in that well defined sulci are present and, except in *O.* (*G.*) *validus,* equally well defined troughs are also present. The sinus originates in a deep fossa, usually in the cephalolateral portion of the sulcus and extends laterally before recurving sharply to the midline; this produces a prominent, tongue-like, laterally oriented ridge which descends toward the lateral parts of the sinus, which latter is frequently partly obscured by an overhang of the cephalolateral prominence and/or lateral extension thereof. These are probably the most complexly organized annuli in the genus.

Further evidence of the digressive nature of the members of this subgenus can be found in the nearly subcylindrical main shaft of the pleopod. Members of the Alabamensis Group are extreme in having a spatulate mesial process with a conspicuous groove along the cephalic face. The hands, although usually not useful for determining relationships, help tie the species together into a cohesive group. In all (except *O. compressus* and *O. chickasawae*) a tuft of setae, of varying degrees of development, occurs at the base of the opposable margin of the fixed finger; in this respect they resemble members of *Crockerinus.* But, most unusual in the genus, fully half of the species have at least one tubercle on the opposable margin of the fixed finger which stands out from the rest in size. Another unusual characteristic occurs in the basal third of the opposable margin of the dactyl (absent only in *O. compressus, O. cooperi* and *O. rhoadesi*): a broad concavity with (except in *O. immunis*) more than one prominent tubercle, structured not unlike that seen in *Cambarus* (*Lacunicambarus*) spp.

Trends leading to Buannulifictus.—More divergent still are members of the subgenus *Buannulifictus.* Except in *O. meeki meeki,* the distal portion of the pleopod is inclined caudally with respect to the main axis of the proximal part of the pleopod, *and* the central projection is curved throughout its length, the apex (except in the same subspecies) directed more or less caudally. The subsetiform mesial process is likewise curved but also from its base takes a path divergent from that of the central projection, the apices of the terminal elements being at least twice as far apart as the bases.

One of the most significant changes in the annulus ventralis was an increase in the cephalocaudal axis. The development of the cephalolateral prominences was more toward a ridge-like oval than toward a circular hillock, a situation shared with *Gremicambarus.* Not surprisingly, the annuli are superficially similar in the two subgenera. But in *Buannulifictus* the lateral development of the prominences is more intrusive on the middle of the annulus, resulting in a sulcus which is more pit-like than ditch-like. At the same time, the mediocephalic incursions of the prominences render the trough poorly evidenced, at best. The sinus originates in a deep fossa near the caudal margin of the cephalolateral prominences, and its peregrinations are not dissimilar to those described for *Gremicambarus,* although a tongue-like ridge as described for the latter subgenus is clearly defined only in *O.* (*B.*) *palmeri palmeri.*

Except for *O.* (*B.*) *palmeri longimanus,* the dactyl concavity typical of *Gremicambarus* is absent, but a tuft of setae at the base of the fixed finger is present, albeit poorly developed, in all but the two subspecies of *O. meeki.* The opposable margins of the fingers usually have well developed tubercles, but no prominently large one is characteristically present. The two subgenera are bound by many commonalities, some of which are apparently synapomorphic. But an equal number of differences exist also. One is led to the conclusion that although their members are rather closely related, they constitute two distinct species groupings, here recognized as subgenera.

Geographic and Temporal Interpretations

In such speculations as have been presented in preceding paragraphs one invariably is led to postulate temporal assignments for proposed events. At the moment I am more prepared to examine geographic relationships than paleontologic ones. Hobbs and Barr (1972) offered explanations of the time and place of the origin of *Orconectes.* They also similarly addressed the early development and migration of the early isolates of the parental population. They accepted the pre-Miocene origin of the genus, located geographically at the southeastern rim of the Cumberland Plateau, proposed by Hobbs (1969), as well as his suggestion that the expansion was essentially westward. Their principal addition was to offer a "Tertiary" northward migration of early populations, some of which gained access to the Atlantic drainages and persisted as *O.* (*F.*) *limosus.* They also provided strong arguments that the genus descended from stream dwellers.

Fitzpatrick (1967) associated emergence of *Crockerinus* and *Procericambarus* with (by inference) the early Quarternary and envisioned subsequent speciation of the former as a result of conditions existing during Illinoian to post-Wisconsin times. His explanations were more compatible with Rhoades' (1962) proposals for events effecting the distribution of northern crawfishes than were those of Hobbs and Barr (1972). Indeed, they rejected outright Rhoades' mechanism to explain the distribution of *O. limosus.*

If I were inclined to disagree with any of the above, I could find no concrete data to refute Hobbs' and Barr's hypotheses. Recently, however, Fitzpatrick (1983) used new geologic information to speculate that a prominent pre-Pleistocene river drained the upper Tennessee into the Florida Parishes of Louisiana and argued that this river could account for the eastern distribution patterns of the Cambarellinae. He carried this proposal further (Fitzpatrick 1986), giving more details, in using such a drainage to account for many peculiarities of crawfish distribution in the eastern part of the Gulf Coastal Plain. In this scheme, the proposed "ancestral home" of *Orconectes* would be related to this river. It seems more than coincidental that the expansion of *Orconectes* is essentially west of this river and that of the early digressives of *Cambarus* (Hobbs 1969) is to the east.

If one uses this proposed river to localize the eastern boundary of the eastcentral margin of the Mississippi Embayment, one can begin to speculate about the dispersal routes (corridors in the sense of Hobbs 1969, 1984). One early group moved north through eastern Tennessee and West Virginia, possibly through the New River system, and gained access into what is now the upper Ohio drainage. From Hobbs' and Barr's (1972) timetable this would be definitely pre-Illinoian and probably Tertiary time. These populations became the members of *Faxonius.* Another "wave" of invasion, out of the same Cumberland source area followed, to diversify into today's *Crockerinus.* This more progressive descendent of the ancestral stock would have obliterated any extant epigean remnant of *Orconectes* (subgenus) and was able to bisect the range of *Faxonius* to leave the probably already isolated *limosus* precursors in the Atlantic drainages and compressing the remainder into three isolated populations near the periphery of a range that at once encompassed the area from the Appalachian divide to the eastcentral rim of the Mississippi embayment and south of the Teays system. By Fitzpatrick's (1967) reckoning this would have occurred before the Illinoian glaciation.

West of what is now the lower reaches of the Tennessee River another stock was establishing itself. This was the precursor of my proposed "Group III" (Fig. 18) lineage (*Billecambarus, Buannulifictus, Gremicambarus, Hespericambarus, Rhoadesius,* and *Tragulicambarus*). These crawfishes seem to have invaded the northern (lower) reaches of this drainage as several "waves"; possibly these are associated with the migrations of the ice sheets of the Pleistocene. One group, however, seems to have become established west of the Mississippi River comparatively early. Exactly how this was accomplished is highly problematical, but surely considerable opportunities exist and existed for animals not too demanding of the stream environment to cross as meanders of the mid-Mississippi channel occur. Apparently the ancestors of members of *Hespericambarus* settled in the Tertiary or early Quarternary streams of northwest Louisiana/Arkansas/Oklahoma and invaded the Quarternary lands as they became available. The present-day representatives east of the river are *O.* (*H.*) *perfectus* and populations very close to it. They, in turn, are almost indistinguishable from Louisiana's *O.* (*H.*) *hathawayi,* and I interpret them to be relatively recent immigrants into the Tombigbee drainage system.

Possibly coincident with these activities, another group was moving up (down by present directions) the streams into the Ohio basin. These diversified into the members of *Rhoadesius* and were more widespread than today. For whatever reason—climatic change, replacement by more efficient competitors, or both—the original range was bisected and remains today as two, essentially relict, allopatric areas.

Two monotypic, enigmataic subgenera attract our attention next. *Orconectes* (*Billecambarus*) *harrisoni* can be found only in a very restricted area just west of the Mississippi River flood plain in Missouri and between the latitudes of confluence of the Missouri and Ohio rivers with the Mississippi. As discussed above, its morphology is very difficult to interpret, but it seems to be most closely related to *Rhoadesius* and could represent a very disparate western isolate from that group of populations. *Orconectes* (*Tragulicambarus*) *lancifer* is likewise morphologically unique and even more difficult to associate with another group of species. That an almost perfect correlation of its distribution with Quarternary-Holocene deposits exists is inescapable, however, and one must therefore assume a comparatively late specialization enabling its almost unique (for *Orconectes*) invasion of the habitats—essentially lentic, often stagnant, or very sluggishly flowing and lacking firm substrates for much of their extent—associated with these regions.

Becoming fully established in the lower (i.e., southern) reaches of the eastern leg (i.e., upper) of the Tennessee River were the progenitors of *Procericambarus.* This may have taken place in Early Quarternary times. This stock seems to have consisted of vigorous competitors; indeed, *O.* (*P.*) *rusticus* is one of the most successful displacers at the present time (Crocker and Barr 1968; Capelli 1975, 1982; Berrill 1978; Capelli and Munjal 1982; Tierney and Dunham 1984). They eliminated *Crockerinus* from its ancestral home on the Cumberland Plateau, drove *O.* (*C.*) *erichsonianus* southward and pushed the second, northern assemblage hard as they invaded the Ohio system. They spread extensively, possibly along the Erigan system, going across the Mississippi to occupy the Missouri highlands and thence southward into the Ouachitas. They tumbled off the Highland Rim into the Nashville Basin to become firmly established in central Tennessee and Kentucky. How this was accomplished will probably always remain unknown. It may have resulted from an invasion down the slopes from the Cumberland Plateau; it may have been via a union of the two segments of the Tennessee River; or it may have been both. Until the approximate time of this fusion to form the present Tennessee River is determined, further speculation seems useless. Man has helped *O.* (*P.*) *rusticus* in its invasions, but much of the range represents its own vigorous and successful expansion into areas breaking free of ice cover.

The lower (southern) parts of the western (lower) leg of the Tennessee drainage saw the nearly simultaneous establishment of ancestors to *Gremicambarus.* Most species initially probably had difficulties expanding their range northward as they encountered the vigorous *Procericambarus* populations and were forced to content themselves with central Tennessee and the emerging lands which are now associated with the Tombigbee River drainage.

To the west and southwest of them *Buannulifictus* fauna was laying claim to most of Mississippi and the southern parts of the west bank of the river. Little conjecture can be made concerning this stock, for present drainage patterns in the critical areas do not well reflect the history of the region. There are extensive "drowned" drainages in northern Mississippi (Murphey and Grissinger 1981), and serious questions of the age and sources of deposits throughout the area have been raised (May 1981, Isphording 1983).

Becoming teleological, one could say that *Gremicambarus* "bided its time" and "worked to build a better mousetrap." By the retreat of the last ice sheet, two species of the subgenus were poised "to hold their own" as the north was exposed for colonization. Surely the subgenus dominates the crawfish fauna of the central part of North America. But an examination of the ranges of the members of the subgenus leaves no doubt that the overwhelming majority of the total range is ococupied by *O.* (*G.*) *immunis* and *O.* (*G.*) *virilis,* the latter exceeded in range only by *Procambarus* (*Ortmannicus*) *acutus* subspp. The several populations of *O.* (*G.*) *virilis, O.* (*G.*) *nais* and *O.* (*G.*) *causeyi* are morphologically nearly indistinguishable, although Pryor and Leone (1952) reported serological differences between *O. nais* and *O. virilis.* The latter has to be evaluated in light of Phillips' report of possible intergrade populations in southwestern Iowa (1980); this is one of the few studies in which a detailed examination for just such a situation has been reported. Regardless, the *Gremicambarus* invaders attempting to move out of Missouri River drainages into southern Missouri and Kansas-Oklahoma were stymied in their southern and southwestern migration by well-established *Buannulifictus* populations and in their westward and northern movements by intolerable or inaccessable habitats resulting from climatic conditions. Nevertheless, they constitute the most widespread subgenus of *Orconectes* and are obviously successful competitors.

In summary, analysis reveals a reasonably rational division of the genus *Orconectes* into 10 subgenera which seem to reflect historical events in the diversification of the genus. Adequate data determining precise relationships are lacking, but generalities implied by the proposed groupings are supported by the information at hand.

Acknowledgments

Many people have contributed to this study, but Horton H. Hobbs, Jr., deserves special recognition. He has been generous with his time and knowledge since he first directed my attention to *Orconectes*. Subsequently, he has made every effort to ease my path toward an understanding of these creatures and crawfishes in general. Raymond W. Bouchard, Horton H. Hobbs III, David Stansbery and their students have given many helpful insights during numerous extended conversations. And not least, personnel of the U.S. National Museum of Natural History consistently worked to make my visits there profitable. To each of these I offer sincere thanks.

Literature Cited

Andrews, E. A. 1906a. The annulus ventralis.—Proceedings of the Society of Natural History of Boston 32:427–480.

———. 1906b. The ontogeny of the annulus ventralis.—Biological Bulletin 10:122–137.

Berrill, M. 1978. Distribution of ecology and seven species of crayfish in southern Ontario.—Canadian Journal of Zoology 56:166–177.

———. 1985. Laboratory induced hybridization of two crayfish species, *Orconectes rusticus* and *O. propinquus*.—Journal of Crustacean Biology 5: 347–349.

Blair, A. P. 1941. Variation, isolating mechanisms, and hybridization in certain toads.—Genetics 26:398–417.

Bouchard, R. W. 1972. A New Genus of Crayfish from Kentucky and Tennessee (Crustacea, Decapoda, Astacidae).—Association of Southeastern Biologists Bulletin 19:56.

———, and J. W. Bouchard. 1976a. *Orconectes saxatilis*, a new species of crayfish from eastern Oklahoma.—Proceedings of the Biological Society of Washington 88:439–446.

———, and ———. 1976b. *Orconectes etnieri*, a new species of crayfish and western Tennessee and northern Mississippi with notes on *Procambarus ablusus* and *Orconectes wrighti*.—Proceedings of the Biological Society of Washington 88: 459–468.

———, and H. H. Hobbs, Jr. 1976. A new subgenus and two new species of crayfishes of the genus *Cambarus* (Decapoda: Cambaridae) from the southeastern United States.—Smithsonian Contributions to Zoology 224:1–15.

Brown, P. L. 1956. A new crayfish of the genus *Orconectes* from Illinois (Decapoda, Astacidae).—American Midland Naturalist 56:163–167.

Bundy, W. F. 1876. *In* S. A. Forbes, List of Illinois Crustacea, with descriptions of new species.—Bulletin of the Illinois Museum of Natural History 1:3, 4, 5, 24–25.

———. 1877. On the Cambari of Northern Indiana.—Proceedings of the Academy of Natural Sciences of Philadelphia 29:171–174.

Capelli, G. M. 1975. Distribution, life history, and ecology of crayfish in northern Wisconsin, with emphasis on *Orconectes propinquus* (Girard). Ph.D. Thesis, University of Wisconsin, Madison, 214 pp.

———. 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard).—Limnology and Oceanography 27:741–745.

———, and J. M. Capelli. 1980. Hybridization between crayfish of the genus *Orconectes*: Morphological evidence (Decapoda, Cambaridae).—Crustaceana 39:121–132.

———, and B. L. Munjal. 1982. Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes*.—Journal of Crustacean Biology 2:486–492.

Chambers, C. L., J. F. Payne, and M. L. Kennedy. 1979. Geographic variation in the dwarf crayfish *Cambarellus puer* Hobbs (Decapoda, Cambaridae).—Crustaceana 36:39–55.

———, ———, and ———. 1980. Geographic variation in the first pleopod of the Form I male crayfish *Cambarellus puer* Hobbs (Decapoda, Cambaridae).—Crustaceana 38:169–177.

Cooper, M. R., and H. H. Hobbs, Jr. 1980. New and little-known crayfishes of the *virilis* Section of the genus *Orconectes* (Decapoda: Cambaridae) from the southeastern United States.—Smithsonian Contributions to Zoology 320:i–iii + 1–44.

Cope, E. D. 1872. On the Wyandotte Cave and its fauna.—American Naturalist 6:406–422.

Cory, L., and J. J. Manion. 1955. Ecology and hybridization in the Genus *Bufo* in the Michigan-Indiana region.—Evolution 9:42–51.

Creaser, E. P. 1931. Three new crayfishes (*Cambarus*) from Puebla and Missouri.—Occasional Papers of the Museum of Zoology, University of Michigan 224:1–10.

———. 1933. Descriptions of some new and poorly known species of North American crayfishes.—Occasional Papers of the Museum of Zoology, University of Michigan 275:1–21.

———. 1934. A faunistic area of five isolated species of crayfish in southeastern Missouri.—Occasional Papers of the Museum of Zoology, University of Michigan 278:1–8.

———. 1962. Notes on the homologies and genetic relationships in the cambarine crayfishes. 7 pages, 22 figures. [Privately printed.]

Crocker, D. W. 1957. The crayfishes of New York state (Decapoda, Astacidae).—New York State Museum and Science Service Bulletin 335:1–335.

———, and D. W. Barr. 1968. Handbook of the Crayfishes of Ontario. University of Toronto Press, Toronto, viii + 158 pp.

Faxon, W. 1884. Descriptions of new species of *Cambarus,* to which is added a synonymical list of the known species of *Cambarus* and *Astacus.*—Proceedings of the American Academy of Arts and Sciences 20:107–158.

———. 1885. A revision of the Astacidae, Part I: The genera *Cambarus* and *Astacus.*—Memoirs of the Museum of Comparative Zoology at Harvard College 10(4):i–vi + 1–186.

———. 1890. Notes on North American crayfishes, family Astacidae.—Proceedings of the United States National Museum 8:356–361.

———. 1898. Observations on the Astacidae in the United States National Museum and in the Museum of Comparative Zoology, with descriptions of new species.—Proceedings of the United States National Museum 20:643–694.

———. 1914. Notes on the crayfishes in the United States National Museum and in the Museum of Comparative Zoology with descriptions of new species and subspecies to which is appended a catalogue of the known species and subspecies.—Memoirs of the Museum of Comparative Zoology at Harvard College 40:351–427.

Fitzpatrick, J. F., Jr. 1963. Geographic variation in the crawfish *Faxonella clypeata* (Hay), with the definition and defense of the genus *Faxonella* Creaser (Decapoda, Astacidae).—Tulane Studies in Zoology 10:57–79.

———. 1965. A new subspecies of the crawfish *Orconectes leptogonopodus* from the Ouachita River drainage in Arkansas.—Tulane Studies in Zoology 12:87–91.

———. 1966a. A new crawfish of the subfamily Cambarinae from Oregon, U.S.A. (Decapoda, Astacidae).—Crustaceana 11:178–184.

———. 1966b. A new crawfish of the genus *Orconectes* from the headwaters of the White River in Arkansas.—Proceedings of the Biological Society of Washington 79:145–150.

———. 1967. The Propinquus Group of the crawfish genus *Orconectes* (Decapoda: Astacidae).—Ohio Journal of Science 67:129–172.

———. 1983. A revision of the dwarf crawfishes (Cambaridae, Cambarellinae).—Journal of Crustacean Biology 3:266–277.

———. 1986. The pre-Pliocene Tennessee River and its bearing on crawfish distribution (Decapoda: Cambaridae).—Brimleyana 12:123–146.

———, and J. F. Payne. 1968. A new genus and species of crawfish from the southeastern United States (Decapoda: Astacidae).—Proceedings of the Biological Society of Washington 81:11–21.

———, and J. F. Pickett, Sr. 1980. A new crawfish of the genus *Orconectes* from eastern New York (Decapoda: Cambaridae).—Proceedings of the Biological Society of Washington 93:373–382.

Fowler, H. W. 1912. The Crustacea of New Jersey. Pp. 29–650 *in* Annual Report of the New Jersey State Museum for 1911.

Girard, C. 1852. A revision of the North American Astaci, with observations on their habits and geographical distribution.—Proceedings of the Academy of Natural Sciences of Philadelphia 6: 87–91.

Hagen, H. 1870. A monograph of the North American Astacidae.—Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College 3:i–vii + 1–109.

Hay, W. P. 1891. The Crustacea of Indiana.—Proceedings of the Indiana Academy of Science 1891:147–150.

———. 1896. The crawfishes of the state of Indiana. Pp. 475–507 *in* 20th Annual Report of the Department of Geology and Natural Resources of Indiana.

———. 1899. Description of two new species of crayfish.—Proceedings of the United States National Museum 22(1187):121–123.

Hobbs, H. H., Jr. 1942. A generic revision of the crayfish of the subfamily Cambarinae (Decapoda, Astacidae) with the descriptions of a new genus and species.—American Midland Naturalist 28:334–357.

———. 1948a. On the crayfishes of the Limosus Section of the genus *Orconectes* (Decapoda, Astacidae).—Journal of the Washington Academy of Sciences 38:14–21.

———. 1948b. Two new crayfishes of the genus *Orconectes* from Arkansas, with a key to the species of the Hylas Group (Decapoda, Astacidae).—American Midland Naturalist 39:139–150.

———. 1948c. A new crayfish of the genus *Orconectes* from southern Tennessee (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 61:85–91.

———. 1949. A new crayfish of the genus *Orconectes* from the Nashville Basin in Tennessee, with notes on the range of *Orconectes compressus* (Faxon).—Proceedings of the Biological Society of Washington 62:17–24.

———. 1951. A new crayfish of the genus *Orconectes* from southeastern Virginia (Decapoda, Astacidae).—Virginia Journal of Science 2:122–128.

———. 1958. The evolutionary history of the Pictus Group of the crayfish genus *Procambarus* (Decapoda, Astacidae).—Quarterly Journal of the Florida Academy of Sciences 21:71–91.

———. 1967. A new crayfish from Alabama caves with notes on the origin of the genera *Orconectes* and *Cambarus* (Decapoda: Astacidae).—Proceedings of the United States National Museum 123:1–17.

———. 1969. On the distribution of phylogeny of the crayfish genus *Cambarus.* Pp. 93–178 *in* P. C. Holt, R. L. Hoffman, and C. W. Hart, Jr., eds., The Distributional History of the Biota of the Southern Appalachians, Part I: Invertebrates. Virginia Polytechnic Institute and State University, Research Division Monograph 1, Blacksburg, Virginia.

———. 1972. The subgenera of the crayfish genus *Procambarus* (Decapoda: Astacidae).—Smithsonian Contributions to Zoology 117:1–22.

———. 1973. New species and relationships of members of the genus *Fallicambarus.*—Proceedings of the Biological Society of Washington 86:461–481.

———. 1974a. Synopsis of the families and genera of crayfishes (Crustacea, Decapoda).—Smithsonian Contributions to Zoology 164:1–32.

———. 1974b. A checklist of the North American crayfishes (Decapoda: Astacidae and Cambaridae).—Smithsonian Contributions to Zoology 166:i–iii + 1–161.

———. 1975 [1976]. Adaptations and convergences in North American crayfishes. Pp. 541–552 *in* J. W. Avault, Jr., ed., Freshwater Crayfish [2]. Louisiana State University Division of Continuing Education, Baton Rouge, Louisiana.

———. 1977. The crayfish *Bouchardina robisoni,* a new genus and species (Decapoda, Cambaridae) from southern Arkansas.—Proceedings of the Biological Society of Washington 89:733–742.

———. 1981. The crayfishes of Georgia.—Smithsonian Contributions to Zoology 318:i–vi + 1–549.

———. 1983. *Distocambarus* (*Fitzcambarus*) *carlsoni,* a new subgenus and species of crayfish (Decapoda: Cambaridae) from South Carolina.—Proceedings of the Biological Society of Washington 96:429–439.

———. 1984. On the distribution of the crayfish genus *Procambarus* (Decapoda: Cambaridae).—Journal of Crustacean Biology 4:12–24.

———, and T. C. Barr, Jr. 1960. Origins and affinities of the troglobitic crayfishes of North America (Decapoda, Astacidae), I. The genus *Cambarus.*—American Midland Naturalist 64:12–33.

———, and ———. 1972. Origins and affinities of the troglobitic crayfishes of North America (Decapoda, Astacidae), II. Genus *Orconectes.*—Smithsonian Contributions to Zoology 105:1–84.

———, and P. H. Carlson. 1983. *Distocambarus* (Decapoda: Cambaridae) elevated to generic rank, with the account of *D. crockeri,* new species, from South Carolina.—Proceedings of the Biological Society of Washington 96:420–428.

———, and J. F. Fitzpatrick, Jr. 1962. A new crayfish of the Propinquus Group of the genus *Orconectes* from the Ohio drainage system in West Virginia (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 75:207–214.

Isphording, W. C. 1983. Interpretive minerology: Examples from Miocene coastal plain sediments.—Transactions of the Gulf Coast Association of Geological Societies 33:295–305.

Jester, D. B. 1967. A new crawfish of the genus *Orconectes* from New Mexico (Decapoda, Astacidae).—American Midland Naturalist 77:518–524.

May, J. E. 1981. The updip limit of Miocene sediments in Mississippi.—Abstracts with Program, Southeastern Section of the Geological Society of America 13(1):29.

Murphey, J. B., and E. H. Grissinger. 1981. Post-Eocene alluvial materials in north-central Mississippi.—Abstracts with Program, Southeastern Section of the Geological Society of America 13(1):31.

Ortmann, A. E. 1905. The mutual affinities of the species of the genus *Cambarus,* and their dispersal over the United States.—Proceedings of the American Philosophical Society 44:91–136.

———. 1931. Crawfishes of the southern Appalachians and the Cumberland Plateau.—Annals of the Carnegie Museum 20:61–160.

Page, L. M. 1985. A new crayfish of the *Orconectes* from the Little Wabash River system of Illinois (Decapoda: Cambaridae).—Proceedings of the Biological Society of Washington 98:564–570.

Penn, G. H., Jr. 1950. A new *Orconectes* from the Pontchartrain watershed in Louisiana and Mississippi (Decapoda: Astacidae).—Journal of the Washington Academy of Sciences 40:381–384.

———. 1952. A new crawfish of the *Virilis* Section of the genus *Orconectes* (Decapoda, Astacidae).—Natural History Miscellanea 109:1–7.

Phillips, G. S. 1980. The decapod crustaceans of Iowa.—Iowa Academy of Sciences Proceedings 87:81–95.

Pryor, C. W., and C. A. Leone. 1952. Serological comparisons of astacuran Crustacea.—Biological Bulletin 103:433–445.

Rafinesque, S. C. 1817. Synopsis of four new genera and ten new species of Crustacea, found in the United States.—American Monthly Magazine and Critical Revue 2:40–43.

Reimer, R. D., and D. B. Jester. 1975. A new crayfish of the genus *Orconectes* from Conchas Lake, New Mexico.—Tulane Studies in Zoology and Botany 19:17–21.

Rhoades, R. 1941. Notes on some crayfishes from Alabama caves, with the description of a new species and a new subspecies.—Proceedings of the United States Museum 91:141–148.

———. 1944. The crayfishes of Kentucky, with notes on variation, distribution and descriptions of new species and subspecies.—American Midland Naturalist 31:111–149.

———. 1962. The evolution of the crayfishes of the genus *Orconectes* Section *limosus* (Crustacea: Decapoda).—Ohio Journal of Sciences 62:65–96.

Smith, D. G. 1981a. A note on the morphological variability of *Orconectes kinderhookensis* (Decapoda: Cambaridae) from the Hudson River system in New York.—Journal of Crustacean Biology 1:389–391.

———. 1981b. Evidence for hybridization between two crayfish species (Decapoda: Cambaridae: *Orconectes*) with a comment on the phenomenon in cambarid crayfish.—American Midland Naturalist 105:405–407.

Tellkampf, T. G. 1844. Ausflug nach der Mammuthhöle in Kentucky.—Das Ausland 171:683–684.

Tierney, A. J. 1982. Individual variation and taxonomic significance of the seminal receptacle of the crayfish *Orconectes propinquus* (Girard) (Decapoda: Cambaridae).—Crustaceana 43:284–296.

———, and D. W. Dunham. 1984. Behavioral mechanisms of reproductive isolation in crayfishes of the genus *Orconectes*.—American Midland Naturalist 111:304–310.

Walls, J. G. 1972. Three new crawfishes related to *Orconectes difficilis* (Faxon) (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 84:448–458.

Williams, A. B. 1952. Six new crayfishes of the genus *Orconectes* (Decapoda, Astacidae) from Arkansas, Missouri and Oklahoma.—Transactions of the Kansas Academy of Science 55:330–351.

Department of Biological Sciences, University of South Alabama, Mobile, Alabama 36688.